Fish growth and degree-days: Advice for selecting base temperatures in both within- and among-lake studies.

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Isaac Newton once said, “if I have seen further, it is by standing on the shoulders of giants.” The metaphor taken to mean that new discoveries are only possible by building on the discoveries of those that have come before. I would like to extend the meaning of this metaphor and say that whatever offering this thesis has to give; it is the cumulative result of all my fortunes in life, of which I have been the recipient of many.

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Dedication

This thesis is dedicated to my parents, Robert J. Chezik and Jill E. Chezik. They have been with me every step of the way with endless love and support. I could not have done this without them.

Abstract

Ectotherm growth and development are largely a function of temperature. Within the range of thermal tolerance, growth and development increases linearly over a mid-range of temperatures. Degree-days (DD; ^{o}C·days) are a method of quantifying the thermal experience of an organism over the linear range and are an increasingly popular method for describing growth and development in fish. To limit degree-day calculations to temperatures within the linear range, a lower temperature threshold (T_o) is incorporated that defines the onset of growth. However, there is currently no convention for choosing T_o and the implications of choosing an inappropriate T_o are largely unknown. This uncertainty has resulted in a wide range of T_o values currently in use both among- and within-species. In this thesis I explore i) how T_o affects the ability of DD to explain within-population variation in fish growth, and ii) the effect of T_o on apparent growth among populations in thermally dissimilar environments. To address these objectives, I first use simulated data to determine the theoretical relationship between T_o and growth. I then demonstrate these theoretical relationships using immature length-at-age data from 8 species and 85 waterbodies in Minnesota USA and Ontario Canada. My results show that DD at low T_o are highly correlated and that these highly correlated low T_o values explain variation in growth equally well within a single population. Furthermore, growth rates among populations of thermally dissimilar habitat become increasingly dissimilar as T_o deviates from the T_o that minimizes the variation in growth rate among populations. This effect is especially apparent when the among-population range in thermal habitats is large. These findings suggest that, although T_o matters little when accounting for variation in growth within a single population, an inappropriate T_o can lead to the appearance of among-population differences in growth. When choosing T_o, I recommend estimating T_o using the Charnov and Gillooly (2003)[1] "10ºC rule" and then rounding to the nearest T_o standard (0, 5, 10 and 15ºC). Choosing a T_o standard in this way will

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[1] Charnov, E.L., and Gillooly, J.F. 2003. Thermal time: body size, food quality and the 10 degree C rule. Evol. Ecol. Res. **5**(1): 43-51.

minimize the effect of T_o error on growth bias in among-population studies. In general, standardization i) simplifies T_o identification, ii) facilitates comparative studies, and ii) promotes the use of DD in future studies.

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Chapter 1

General introduction: Growth, temperature and degree-days in fish science

Fish growth can be defined as the investment of surplus energy into the production of somatic or reproductive tissue. Although growth is often defined in these simple terms of energy transfer, as a life history trait growth may be the single most important predictor of fish survival and fitness (Jonsson and Jonsson 2011). For instance, size is positively correlated with juvenile survival (e.g., Sogard 1997), adult female egg abundance (e.g., Morita and Takashima 1998) and male reproductive success (e.g., Magnhagen and Kvarnemo 1989). These growth-dependent mechanisms act to regulate population dynamics (Lorenzen and Enberg 2001) and determine when fish recruit into a fishery. Therefore, by understanding growth, we gain insight into the "health", quality and economic stability of our fisheries (Hubert and Quist 2010).

Fish are poikilotherms meaning that their growth, and the underlying processes therein, are predominately determined by the temperature of their environment when food is not limiting (Diana 1995). The inability of fish to maintain thermal homeostasis, as their thermal environment fluctuates, is largely a result of their relatively low metabolic rate, lack of insulation and countercurrent lamellar blood flow (Beitinger 2000). In general, fish growth is linear over a midrange of temperatures (Sharpe and DeMichele 1977) because the rates of the chemical reactions that result in metabolism are temperature dependent (Jobling 1994). In this way, fish growth and ambient temperature are inextricably linked (e.g., Weatherley and Gill 1987).

Because ambient temperature controls fish growth it is considered an ecological resource (Magnuson et al. 1979), and can be quantified using a degree-day approach. The degree-day, first introduced as thermal time by René Antoine Ferchault de Réaumur in 1735 (Rittner 2009), quantifies the thermal opportunity for growth by aggregating temperatures relevant to growth. A single degree-day (DD; ^{o}C·days) is calculated as

(1.1) $$DD = \left[\frac{T_{Max}+T_{Min}}{2}\right] - T_o$$

where T_{Max} and T_{Min} are the maximum and minimum daily ambient temperature, respectively, and T_o is the temperature below which growth or development does not occur (often referred to as the base or threshold temperature). When positive degree-day values are summed over some period of interest, the resultant cumulative degree-days act as an index of the metabolically relevant thermal energy that was experienced over that period.

The degree-day assumes growth to be linear with and solely a function of temperature (Legg 1998a). Although fish growth is non-linear at the extremes of their thermal limits (e.g., Edsall 1993), the majority of growth typically takes place in the linear region. Also, it is well understood that there are temperature independent regulators of growth (i.e., population density, genetics, pH, trophic state, etc.), and a complete growth model would include such variables. On the other hand, assuming temperature is the only contributor to growth allows degree-days to uniquely account for temperature dependent processes. In this way, unexplained variation can be attributed to factors that are independent of temperature (e.g., population density, Venturelli et al. 2010). Ultimately, neither assumption impinges on the degree-days ability to account for temperature dependent growth.

The degree-day greatly outperforms calendar time when describing concurrent patterns of growth and development because it directly measures the thermal opportunity for growth, which can vary over time and across latitude or altitude. For example, in agronomy when predicting the fifth-leaf stage of wheat, a calendar-based model is accurate within nine days whereas a degree-day model is accurate to within two days (Miller et al. 2001). Similar increases in precision have been shown in fish science. For instance, Colby and Nepzy (1981) demonstrated that variation in interspecific growth rates among walleye (*Sander vitreus*) populations was best described using degree-days rather than calendar time. In marine systems, Neuheimer and Taggart (2007) showed that length-at-age in 17 stocks of North Atlantic cod (*Gadus morhua*) was significantly correlated with degree-days, accounting for 93% of the variation in length-at-age. Calendar time failed to detect a significant correlation in these same data.

Although the degree-day approach is superior to calendar time when describing growth, degree-days continue to be underutilized in fish science, accounting for only 5% of temperature-related growth studies between 1980 and 2006 (Neuheimer and Taggart 2007). It is unclear why fish science has been reluctant to adopt the degree-day given that the relationship between temperature and development in fish is well understood (e.g., Morrow and Mauro 1950, Paloheimo and Dickie 1966, Fry 1971, Kitchell et al. 1977) and the degree-day approach has been widely used in agronomy for 270+ years (e.g., Réaumur 1735, cited in Bonhomme 2000).

Two likely reasons why degree-days have been underutilized in fish science include, i) a general reluctance to depart from the convention of calendar time and ii) prohibitive limitations inherent in collecting water temperature data. The latter is understandable if the efficacy of the degree-day were dependent on precisely measuring the thermal experience of fish. If so, not only would temperature need to be recorded at multiple depths but also in several locations in order to account for within lake variability (Stevens et al. 1978). Furthermore, because fish exhibit behavioral thermo-regulation (Neill and Magnuson 1974), individual locality data would also be essential. These limitations in water temperature may explain why early degree-day studies were restricted primarily to egg development and aquaculture (Wallich 1901), where temperature is easily monitored and controlled.

It is now understood that air temperature is highly correlated with surface water temperature and acts as a suitable surrogate when water temperature data are incomplete or absent (e.g., Kumar et al. 2013, Livingstone and Lotter 1998, Macan and Maudsley 1966). The availability of air temperature data allows for and has resulted in comparative growth studies among populations and over large areas (e.g., Rypel 2012a,b). A review of the literature shows that while there is a general trending increase in growth studies using degree-days, comparative studies are becoming more common and almost exclusively use air temperature data (Fig. 1.1). At the same time, within population studies are not increasing as rapidly and continue to rely heavily on water temperature data. Although there is no evidence suggesting the efficacy of water temperature to be greater than that of air, this dichotomy in study type suggests water temperature is preferred when available while air temperature is an acceptable alternative. Between the adoption of air temperature as a water temperature surrogate and water temperature records becoming more complete, the degree-day is becoming much more popular. Given its utility and efficacy it is likely to become a standard tool for describing fish growth and development.

Although the degree-day is becoming more widely used in fish science, little has been done to understand its shortcomings and pitfalls, nor have standards or methods been developed to maximize its utility. For instance, it is unclear what temperatures act as lower and upper bounds to growth and whether the precision of these values affect the degree-days efficacy. Furthermore, although degree-days and annual immature growth exhibit a linear relationship, this has yet to be shown for within season immature growth. Simple questions of whether air temperature is truly a good surrogate for water temperature or whether degree-days estimate the growth of warm-water and cool-water species equally well have yet to be understood. By taking the time now, during the degree-day's infancy in fish science, we can avoid developing unsubstantiated conventions that leave datasets incompatible, results inaccurate, and conclusions incorrect.

My thesis takes the first steps in defining the bounds to describing fish growth when using degree-days. It does this by looking critically at the effect of T_o when accounting for variation in growth and when comparing growth among populations. Currently there is no common method in use for defining T_o, rather these values are often chosen with either no justification or are generalized to the minimum temperature for a given physiological process. In entomology, several methods have been developed to empirically estimate T_o values (Arnold 1959), but these have received limited use in fish science. This is concerning because aggregating degree-days before or after the initiation of growth results in an inaccurate description of growth-rate. Minimizing the statistical noise that results from our methods enhances our ability to detect real differences over time or among populations and limits type II errors (i.e., false positives). In chapter 2, I explore how the description of the growing season changes with T_o, and the effect of T_o on explained variation in growth. Chapter 3 builds on the previous chapter by understanding the effect of T_o on apparent growth rates among lakes over a thermal gradient. In both chapters simple conceptual models are used to develop clear predictions and hypotheses, which are then tested using empirical length-at-age data aggregated from databases in Minnesota and Ontario.

Chapters 2 and 3 have been prepared as manuscripts for publication in the Canadian Journal of Fisheries and Aquatic Sciences (CJFAS). At the time of this writing, Chapter 2 had been accepted with minor revisions but those revisions had yet to be submitted and therefore will be referred to as Chezik et al. (*in review*). Publication of these chapters by the University of Minnesota is allowed under the 'author rights' provided by CJFAS. These rights state, "authors may reuse all or part of their manuscript in other works created by them for noncommercial purposes, provided the original publication in an NRC Research Press journal is acknowledged through a note or citation". Although Chapter 2 is not yet published the DOI for this paper will be 10.1138/cjfas-2013-0295 and can be found at the CJFAS website upon acceptance. Co-authors on these manuscripts include Nigel P. Lester and Paul A. Venturelli. I will use the plural pronouns "we" or "our" instead of the singular "I" or "my" in reference to co-authorship.

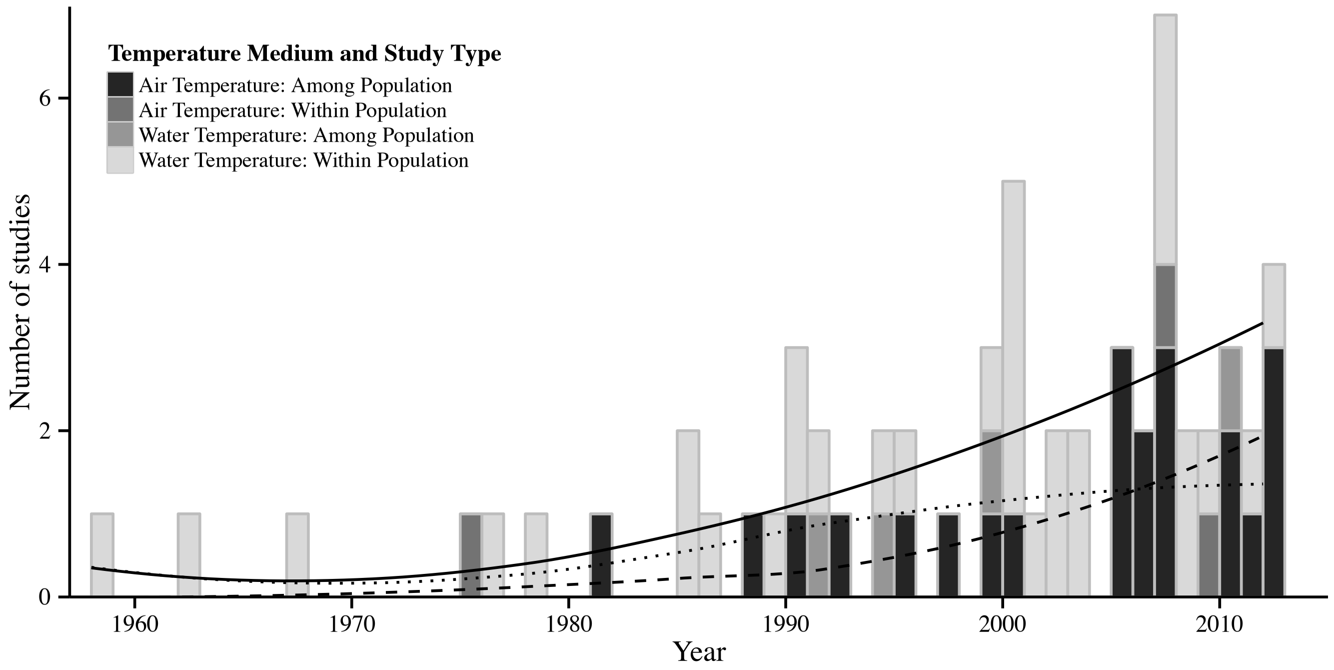

Figure 1.1 The frequency of freshwater studies over time using degree-days to i) account for growth within a single population or localized region and ii) compare growth among thermally disparate populations, using either water or air temperature. Overall, the number of growth studies using degree-days is increasing (-) along with the use of air temperature as a surrogate for water temperature (--), recently surpassing water temperature based studies (•••). All trends described by a loess smoother (α = 1).

Chapter 2

Fish growth and degree-days I: Selecting a base temperature for a single population study.

Synopsis

Degree-days (DD) are an increasingly popular method for explaining variation in fish growth and development. By including a base temperature (T_o) the DD formula limits calculations to temperatures that are relevant to growth. However, a review of growth studies shows multiple T_o values in use for a given fish species. To determine how T_o affects the ability of DD to explain within-population growth variation, we first show that the ability of DD to describe a growing season is robust to low values of T_o. We then analyzed immature length data from 8 species and 85 waterbodies in North America to show that there is a broad range of T_o values that effectively explain growth variation. Based on these results, we argue that precise T_o estimates are unwarranted for most single-population studies, and recommend standard T_o values (0, 5, 10, 15^{o}C). Standardization facilitates comparative studies and promotes the use of DD in future research. To this end, we provide equations for converting annual DD at a given T_o to annual DD at a standard T_o.

2.1 Introduction

The metabolic rate of fish and other ectotherms is largely determined by the ambient temperature of their environment (Hazel and Prosser 1974) and increases linearly over a midrange of temperatures (Sharpe and DeMichele 1977). The amount of mid-range ambient thermal energy that an ectotherm has experienced can be quantified using a degree-day approach (also known as thermal time, e.g., Trudgill et al. 2005). The degree-day for a single day (DD; ^{o}C·days) is calculated as

$$DD = \left[\frac{T_{Max}+T_{Min}}{2}\right] - T_o, \qquad (2.1)$$

where T_{Max} and T_{Min} are the maximum and minimum daily ambient temperature respectively and T_o (often referred to as the base or threshold temperature) is the temperature below which growth or development is non-linear and effectively zero. When non-negative DD values are summed over some period of interest, the resultant cumulative degree-days at a given T_o (CDD_{To}; ^{o}C·days) is an index of the metabolically relevant thermal energy that was experienced over that period. This index is useful for describing concurrent patterns of growth and development (e.g., Neuheimer et al. 2012, Venturelli et al. 2010).

Although degree-days have been used for decades to describe growth and development in plants (e.g., Réaumur 1735, cited in Bonhomme 2000) and insects (e.g., Seamster 1950, Thorup 1963), this approach is rare in fish science, accounting for only 5% of all temperature-related growth studies between 1980 and 2006 (Neuheimer and Taggart 2007). Relationships between temperature and development in fish are well understood (e.g., Morrow and Mauro 1950, Paloheimo and Dickie 1966, Fry 1971, Kitchell et al. 1977), but for decades the degree-day approach was limited to egg development (e.g., Wallich 1901). Degree-days were first applied to growth by Le Cren (1958), but it wasn't until the late 1970's that this application began to increase in popularity (Fig. 1.1). This increase appears to have been facilitated by the use of air temperatures as a surrogate for surface water temperatures (e.g., Ney and Smith 1975, Colby and Nepszy 1981). Air temperatures are highly correlated with surface water temperatures (e.g., Macan and Maudsley 1966, Reuter et al. 2009) and air temperature records are typically more extensive and complete. Therefore, air temperatures permit growth studies over large spatial and temporal scales (e.g., Purchase et al. 2005, Wagner et al. 2007, Latta et al. 2008) and when local time series of water temperature are incomplete or unavailable (e.g., Rennie et al. 2009, David 2012, Rypel 2012a,b).

The degree-day approach to describing fish growth is increasing in popularity, but a review of the freshwater literature shows a diversity of methods for estimating T_o and a diversity of T_o values in use for a given species (Table 2.1). More often than not, T_o values are used without justification. When justification is provided, it is usually that T_o was i) based on the minimum temperature for some physiological process (growth, feeding, spawning, etc.), ii) estimated via model fitting (e.g. bioenergetics, regression), or iii) taken from other (sometimes unrelated) fishes or even plants (Table 2.1). Among freshwater species, reported values of T_o range from -3.6°C for smelt (*Osmerus eperlanus*) to 18°C for spotted gar (*Lepisosteus oculatus*). Within species, T_o can range from 0 to 14°C (yellow perch, *Perca flavescens*; European perch, *P. fluviatilis*) and take as many as 7 different values (roach, *Rutilus rutilus*; Table 2.1). This diversity appears to be due, in part, to a tendency to estimate T_o anew rather than to adopt an existing estimate (Table 2.1).

There are at least four potential reasons to be concerned about the inconsistency with which T_o values for fish growth are being estimated (or simply adopted). First, different approaches to estimating or justifying T_o are likely to lead to different values, even for the same population. For example, T_o for roach in a Dutch lake was 11.5°C in the lab, 10.2°C when fitting a growth model to field data, and 17.5°C when using this model to predict growth in the field (Table 2.1). Second, the same estimation method can yield different T_o values for different populations (e.g., goodness of fit applied to roach; Table 2.1), which suggests that we must estimate T_o for every population. Third, different T_o values can lead to differences in the ability of degree-days to explain or predict growth. These differences arise because T_o determines the extent to which degree-days integrate thermal energy that is relevant to growth. This point argues for the adoption of a single, robust estimation method across studies, and cautions against adopting T_o values from different species. Finally, variation in T_o hinders the comparison and interpretation of degree-days and growth rates among populations and studies. For example, whereas Abbey and Mackay (1991) reported a yellow perch growth rate of 0.02 mm/ºC·Day using T_0, Power and van den Heuvel (1999) reported 0.09 mm/ºC·Day when using $T_{13.5}$.

In this study we address potential concerns over variation in T_o among within-lake studies of degree-days and growth. Specifically, we use simulated and empirical data to i) determine how variation in T_o affects the ability of degree-days to account for within-lake variation in immature growth, and ii) identify the scope for standardized T_o values in future within-lake growth studies. Our interest is in T_o from an applied rather than a theoretical perspective. In theory, there is a precise, species- or population-specific temperature below which growth rate is effectively zero (Charnov and Gillooly 2003) and it is therefore appropriate to set T_o to this value. However, if the ability of degree-days to explain growth is robust to T_o, then, from an applied perspective, it is appropriate to abandon precise T_o estimates in favour of a standardized value or set of values.

2.2 The effect of T_o on degree-days

A logical first step in determining how the degree-days ability to explain growth changes with T_o is to determine how degree-days themselves change with T_o. To this end, we assumed that annual temperature cycles are well approximated by a sine curve (Arnold 1959, Shuter et al. 1983). Annual degree-days above some T_o (ADD_{To}; ^{o}C·days) are then given by the area under this curve (Baskerville and Emin 1969):

$$ADD_{\mathrm{To}} = \frac{365}{\pi}\left[w\int_{\theta}^{\frac{\pi}{2}} \sin t\, dt - \int_{\theta}^{\frac{\pi}{2}} (T_o - T_{Mean})dt\right], \tag{2.2}$$

where *t* is day in year, 365 is the cycle period, $w = \frac{T_{Max} - T_{Min}}{2}$, T_{Mean} is mean annual temperature and $\theta = \frac{T_o - T_{Mean}}{w}$ (Fig. 2.1a). To determine the effect of T_o on ADD_{To}, we used equation 2.2 to calculate ADD_{To} for all integer values of T_o in the range 0 to 30^{o}C, and for four values of *w* (15, 20, 25 and 30 ^{o}C). Increasing the threshold (T_o) decreased the summable area under the curve (i.e., ADD_{To}) and increasing *w* increased available thermal energy (i.e., decreased latitude). For each *w*, we then expressed each value of ADD_{To} as a proportion of ADD_{To-1} (Fig. 2.1d). Results suggest that $ADD_{To} \approx ADD_{To-1}$ for a range of T_o values $\geq 1^{o}$C, and that the extent of this plateau increases with *w* (Fig. 2.1d).

In other words, a 1ºC change at low T_o results in relatively similar ADD_{To} values while a 1ºC change at high T_o results in relatively different ADD_{To} values. We observed a similar pattern in both air (Fig. 2.1b and Fig. 2.1e) and water (Fig. 2.1c and Fig. 2.1f) temperature data from the Gulf Coast to Alaska. Overall, these results suggest that our ability to describe a growing season using degree-days is largely robust to T_o regardless of medium, provided that T_o is not too large (or w is not too small).

2.3 The effect of T_o on explained variation in growth

If our ability to describe a growing season using degree-days is robust to T_o, then our ability to use degree-days to explain growth within a population should also be robust to T_o. To test this hypothesis, we compiled fish and temperature data from Ontario Canada and Minnesota USA, and regressed cohort length at age of each population against cumulative degree-days for a range of T_o values. We used the coefficient of determination (r^2) of each length|degree-day regression as a measure of the effect of T_o on explained variation in species-specific growth within a waterbody. This method has been developed independently by Baras and Philippart (1999) and Neuheimer and Taggart (2007), and was applied to a population of walleye by Venturelli et al. (2010). We used the goodness of fit (r^2) approach and empirical rather than simulated growth data to test our hypothesis because i) the r^2 approach allowed us to both identify and evaluate the performance of each T_o value, ii) empirical growth data integrate both direct (i.e., metabolic) and indirect (i.e., productivity-based) temperature effects, and iii) we are ultimately interested in the ability of degree-days to explain growth in natural environments.

2.3.1 Methods

i) *Fish data*

We created a database of individual fish records that combined the Ontario Ministry of Natural Resources (OMNR) fall walleye index netting (FWIN) database (1993-2008) with the Minnesota Department of Natural Resources (MNDNR) statewide database (2001-2011) and supplemental data (2001-2011) from Minnesota's ten large lakes (Winnibigoshish, Rainy, Vermillion, Leech, Cass, Pepin, Mille Lacs, Kabetogama, Lake of the Woods, and Upper Red Lake). Minnesota data were collected between March and December using a variety of methods (e.g., electrofishing, gillnetting, trap-netting, trawling, trot-lining, seining, angling). Ontario data were collected between September and November using multi-mesh gillnets set overnight at multiple depths (Morgan 2002).

For each fish we were interested in the following information: waterbody, sample date (day, month and year), species, age (years), total length (L; mm), maturity and aging structure. We focused on immature fish so that our analyses of somatic growth were not confounded by the allocation of surplus energy to reproduction. This approach can create a small bias in the growth trajectory if it removes the fast-growing (i.e., early-maturing) fish from the oldest cohort(s). We also focused on fish that were aged using a reliable aging structure or sampled at the start or end of the growing season. We avoided unreliable aging structures because the accuracy of the degree-day assignment depended on the accuracy of age estimates (see next section). We assigned reliability to different aging structures using a combination of expert opinion (Mike McInerny MNDNR 23070 N. Lakeshore Dr. Glenwood, MN 55041, Susan Mann OMNR 479 Government Rd. PO Box 730 Dryden ON P8N2Z4) and the literature (Campbell and Babaluk 1979, Graeb and Willis 2010, Schneider 2001, Soupir et al. 1997, Trippel and Harvey 1991). For example, we assumed that only age-0 fish were accurately aged in the field, and that only walleye ≤age-5 were accurately aged using scales. We also used expert opinion (MNDNR) to define the growing season as June through August, inclusive. We avoided records that were sampled during this period because there is currently no validated protocol for combining whole- and partial-season degree-days in a single analysis.

Our final database contained 47,486 fish records representing 8 species from 64 waterbodies in Ontario Canada and 21 waterbodies in Minnesota USA (Table 2.2). Walleye comprised the majority of the database (86% of all fish) followed by other percid species (14%).

ii) *Temperature data*

We assigned CDD_{To} values to each fish by summing the annual degree-days that each fish experienced prior to capture. This approach required time series estimates of ADD_{To} for each waterbody. For waterbodies in Minnesota, we calculated ADD_{To} time series

(2001-2011) using 100 km^2 resolution maps of kriging-interpolated air temperature data (T_{Min} and T_{Max}). These data were collected from automated weather stations owned and operated by the National Weather Service, and assembled and processed by the Minnesota State Climatology Office-MNDNR. We calculated ADD_{To} by applying equation 2.1 to daily T_{Min} and T_{Max} values from the grid point closest to the centroid of the waterbody of interest, and then summing across non-negative DD values in that year. Because our objective was to determine the effect of T_o on explained variation in growth, we repeated these degree-day calculations for each integer value of T_o in the range 0-30^{o}C (the range of water temperatures that a temperate, freshwater fish is likely to experience in a given growing season). Thus, we generated a unique time series of ADD_{To} values for all waterbodies and T_o values. For waterbodies in Ontario, we obtained ADD_{To} time series (1981-2008) using the Historical Climate Analysis Tool (Cross et al. 2012), which automatically applied the above protocol to 1 km^2 resolution maps of kriging-interpolated T_{Min} and T_{Max} data.

We used age, together with capture year and month, to determine the CDD_{To} that each fish experienced prior to capture. Because fish are aged to a January 1 birthday (Holden and Raitt 1974), we used different summation rules for different capture months. For fish captured during the period January to May (i.e., after their common birthday but before the start of a growing season), we summed ADD_{To} across the previous *n* growing seasons, where *n* is the age of the fish in years. Thus, if a 2 year-old fish was captured in January 2005, we calculated CDD_{To} as the sum of ADD_{To} values from 2003 and 2004. For fish captured during the period September to December (i.e., before their common birthday but after the previous growing season), we calculated CDD_{To} by summing ADD_{To} across the previous *n*+1 growing seasons, beginning with the current year of capture. Thus, if a 2 year-old fish was captured in September 2005, we summed ADD_{To} values from 2003 to 2005.

iii) *Statistical analyses*

Our analyses included populations for which we had ≥5 cohorts distributed over ≥3 age classes that each contained ≥5 individuals (sexes combined). We set these minima to ensure that growth was accurately described and not unduly influenced by outliers. For each population, we calculated mean length-at-age for each cohort. Here ‘cohort’ refers to an age-class observed during a sampling event rather than a group of fish that hatched in the same year. This means if we had multiple years of data for a given population, a single age class typically had several mean length estimates (e.g., Fig 2.2). We assumed the length (L) of immature fish could be described by a linear model

$$L = m \cdot CDD_{T_o} + b \tag{2.3}$$

where CDD_{To} is the thermal age for a given T_o. We used ordinary least squares to estimate parameters m and b and the coefficient of determination (r^2) for a range of T_o values (0 to 30ºC) – see example in Fig. 2.2. We then plotted r^2 against T_o to examine how goodness of fit varied with temperature threshold.

Statistically speaking, the relative goodness of fit of different models should be evaluated using AIC because r^2 is i) an inappropriate method for comparing models when the range of the explanatory variable varies among models (which was the case in our study), and ii) biased towards models with large ranges in the explanatory variable (Maindonald & Braun 2007). However, whereas both approaches produced qualitatively (and almost quantitatively) identical results, r^2 also quantifies the strength of the relationship and there is precedence for this approach (Baras and Philippart 1999, Neuheimer and Taggart 2007, Venturelli et al. 2010).

2.3.2 Results

Across species and waterbodies (Fig. 2.3), the r^2 method revealed a wide range of T_o values that were effective at describing growth. For all eight species in our database, r^2 values were similar for small values of T_o. Beyond this plateau r^2 dropped off quickly or became erratic. Erratic behaviour at high T_o was common for species or waterbodies that had low sample sizes (i.e., few cohorts or fish per cohort). This plateau in r^2 was evident in all 81 walleye populations in our analysis and had a median value of 14^{o}C (range 6-21^{o}C) (Fig. 2.4). Although Fig. 2.1 suggests that the length of the r^2 plateau increases with the length of the growing season and w in equation 2.2, we found no evidence in walleye that r^2 increased over the mean ADD_0 range (2157-3733^{o}C·days) (df=79,

r^2=0.04, p-value=0.062). Visual inspection of each regression and associated diagnostic plots indicated the assumptions of the linear model were met.

2.4 Discussion

In the Introduction, we described four concerns over the inconsistency with which T_o values are being estimated (or adopted) in within-lake growth studies: i) different approaches applied to the same population are likely to lead to different T_o values, ii) identical approaches applied to different populations are likely to lead to different T_o values, iii) different T_o values can lead to differences in the ability of degree-days to explain or predict growth, and iv) variation in T_o hinders the comparison and interpretation of degree-days and growth rates among populations and studies. Our results suggest that, from an applied perspective, concerns i-iii are largely unfounded; within a given waterbody, there is a broad range of T_o values that are almost equally effective at explaining variation in growth. This pattern was consistent across the 8 freshwater species (Fig. 2.3) and among the 81 walleye populations in this study (Fig. 2.4). It was also apparent in 21 other freshwater and marine species (Baras and Phillippart 1999, supplemental material for Neuheimer and Taggart 2007). This broad range of effective T_o values has little to do with limitations on growth at temperatures approaching 0°C. Rather, it stems from an inherent property of the degree-day approach, namely that ADD_{To} values become increasingly similar as T_o approaches 0°C (Fig. 2.1). These results suggest that there is little benefit in precisely estimating T_o when describing growth within a waterbody. Indeed, given that T_o estimates are likely to vary across methods, populations, and species (Table 2.1), increased precision is costly in that it complicates comparisons across populations and studies (concern iv).

The lack of a need to precisely estimate T_o for a given waterbody and the benefit of being able to compare results across populations and studies provides ample scope for adopting standard T_o values when describing fish growth. To this end, we recommend standardized T_o values of 0, 5, 10, and 15°C for growth studies involving freshwater fishes in temperate and arctic waterbodies. These standards are widely used in agronomy and entomology (Pruess 1983) and are common in engineering (e.g., heating and cooling degree-days). As such, air temperature-based degree-day data for each of these standards are widely available. These standards should apply equally well to marine fishes (at least in temperate and arctic waters; supplemental material for Neuheimer and Taggart 2007) and processes other than growth (e.g., maturation) because the correlation between ADD_{To} is an inherent property of the degree-day.

Standardization does not imply that a single threshold model is the best way to account for variation in growth. The bioenergetics literature clearly shows that growth in fish is a complex function of temperature rather than the simple step function that is assumed by the degree-day approach: growth rate typically increases as temperature approaches an optimal value and then declines as temperature exceeds the optimum (e.g., Kitchell et al 1977, Hanson et al. 1997 – Wisconsin Bioenergetics model). Although a single threshold model can approximate the rise in growth with temperature, it does not account for a reduction at high temperature. Thus, the single threshold degree-day approach assumes that more heat is always better. However, standardization is appropriate for the degree-day approach because there is a range of T_o values that effectively explain growth in a given species, and these ranges of values overlap considerably among species (Fig. 2.3). We provide multiple standardized values so as to accommodate the disparate thermal preferences among species (e.g. cold-, cool-, and warm-water species; Magnuson et al. 1979) and simplify the task of assigning a single T_o to a given species or community.

To facilitate the use of 0, 5, 10, and 15°C as T_o standards in fish science, we used air-based annual degree-day data from 303 waterbodies in Ontario for the period 1981-2008 (n = 8484 waterbody years) to derive the following linear conversion equation:

(2.4) $$ADD_{T_{o},y} = i + s \cdot ADD_{T_{o},x}$$

(2.5) where $$i = a_4 \cdot T_{o,x} + a_5,$$

(2.6) $$s = \begin{cases} a_1 \cdot T_{o,x} + a_2, \ T_{o,y} = 0 \\ \frac{1}{a_1 + a_2 \cdot {T_{o,x}}^{a_3}}, T_{o,y} > 0 \end{cases},$$

$ADD_{T_{o,x}}$ is observed annual degree-days, $T_{o,x}$ is the T_o value being converted from, $ADD_{T_{o,y}}$ is predicted annual degree-days at the $T_{o,y}$ standard of interest (0, 5, 10, or 15°C), and a_1- a_5 are constants (Table 2.3). Because we estimated parameter values using $ADD_{T_{o,y}}|ADD_{T_{o,x}}$ relationships for which r^2 was ≥0.90, each standard $T_{o,y}$ model has an $\widehat{ADD}_{T_{o,y}}|ADD_{T_{o,y}}$ r^2 of 0.91±0.006 provided that $T_{o,x}$ and $ADD_{T_{o,y}}$ are within prescribed range limits (see Table 2.3). Without further study we recommend against using equation 2.4 to convert among degree-days based on water temperatures. Although air and water temperatures are both highly correlated at a given location and well approximated by a sine curve (Fig. 2.1), these sine curves and the ADD_{To} values that result from them are different because annual air and water profiles do not share the same T_{Mean}, w or cycle period.

The argument for adopting standardized base temperatures when applying degree-days to fish growth is essentially this: if one is interested in using degree-days to describe growth, and the ability of degree-days to describe growth is robust to T_o (as we have shown), then the benefits of standardizing T_o far outweigh the costs. We acknowledge that standardization can result in a marginal reduction in explanatory and predictive power and will certainly preclude certain types of analyses (e.g., among-species comparisons of the extent to which degree-days explain growth). However, standardization eliminates the need to identify T_o values for each population and study, facilitates comparative studies, and promotes the use of degree-days in future research. When the use of a standard T_o value is untenable, our advice is to follow published precedent. Following precedent for identifying T_o values relevant to growth should ensure a modicum of standardization. If T_o must be estimated with precision then we recommend setting T_o to the minimum temperature for growth. Methods for estimating T_o in this way are described in relevant references in Table 2.1; see also Charnov and Gillooly (2003), Gagné and Rodríguez (2008) and Legg et al. (1998a).

In this study, we showed that the ability to describe fish growth in a single population is robust to T_o and that there is scope for adopting standard T_o values that are already in use in agronomy and entomology. However, it remains to be tested whether these results hold when describing fish growth in multiple populations or over large spatial scales (e.g., marine stocks). Until this work is complete, we caution that precise T_o

might be necessary in certain studies. We also encourage research to determine the extent to which our results hold at more southern latitudes, and under what circumstances we should include thermal maxima in degree-day calculations. Similarly, further research is needed to determine why cisco growth in Leech Lake was best explained using a T_o of ~20^{o}C (Fig. 2.3b). Given that cisco exhibit optimal growth at 18.1ºC and prefer 8.7 to 16.1ºC (Hasnain 2013), this result is likely a statistical anomaly stemming from a relatively small sample size. Regardless, it appears that growth in this population is relatively poorly described by air temperature derived degree-days, and we wonder if this trend is evident in other populations and cold-water species. In general, there is also a need to develop protocols for combining whole- and partial-season degree-days in a single analysis, and for converting among T_o values when degree-days are based on water temperature. Clearly there is still much to learn about the use of degree-days in fish science and we encourage more research to address these and other questions.

Table 2.1 A summary of published T_o values used in growth studies of freshwater fishes within a single waterbody or localized region. Adoption frequency refers to the number of times that an estimated T_o value was adopted in later studies involving the same species.

scientific name	common name	age(s)[a]	T_o (ºC)	temperature[b]	justification[c]	reference	adoption frequency
Abramis brama	common bream	0	12.8	W	1	Mooij et al. (1994)	2
Aplodinotus grunniens	freshwater drum	1-10	9.0	W	2	Braaten and Guy 2002	0
Barbus barbus	barbel	0	13.5	W	3	Baras and Philippart (1999)	0
Carassius carassius	crucian carp	0-2	12.0	W	4	Copp et al. (2008)	1
Carpiodes carpio	river carpsucker	1-8	10	W	2	Braaten and Guy (2002)	0
Coregonus clupeaformis	lake whitefish	2-3	5	A	9	Rennie et al. (2009)	0
Esox lucius	northern pike	juvenile	7	W	2	Bry et al. (1991)	0
		unknown	10	W	5	Frost and Kipling (1967)	3
Gobio gobio	gudgeon	0	12	W	9	Cowx (2000)	0
Gymnocephalus cernua	ruffe	0	7.6	W	1	Mooij et al. (1994)	0
Lepomis gibbosus	pumpkinseed sunfish	0	14	W	2	Murphy et al. (2012)	0
Lepomis macrochirus	bluegill sunfish	0	14	W	2	Murphy et al. (2011)	0
Leuciscus leuciscus	common dace	0	12	W	9	Cowx (2000)	0
		0	12	W	3	Mills and Mann (1985)	4
Lota lota	burbot	1-3	0[d]	W	9	Kjellman and Eloranta (2002)	0
Macrhybopsis meeki	sicklefin chub	1-2	10	W	2	Braaten and Guy (2002)	0
Micropterus salmoides	largemouth bass	0	0	W	9	Schlosser et al. (2000)	0
Morone americana	white perch	0	15	W	2	O'Gorman and Burnett (2001)	0
Notropis atherinoides	emerald shiner	1-2	7	W	2	Braaten and Guy (2002)	0
Oncorhynchus clarkii	cutthroat trout	0	5	W	2	Coleman and Fausch (2007a)	1
Osmerus eperlanus	smelt	0	-3.6	W	1	Mooij et al. (1994)	1
		1-2	5	A	7	Power and Attrill (2007)	0
Perca flavescens	yellow perch	0	0	W	2	Mills et al. (1989)	0
		0	4.4	A	9	Ney and Smith (1975)	0
		0	10	A	9	Ney and Smith (1975)	0
		2-4	14	W	5	Henderson (1985)	0
		0	13.5	W	5	Tardif et al. (2005)	0
Perca fluviatilis	European perch	1	0[d]	W	9	Borcherding and Magnhagen (2007)	1
		0	9.8	W	1	Mooij et al. (1994)	4

Table 2.1 Continued

		0	14	W	9	Griffiths and Kirkwood (1995)	0
		1-14	14	W	2	Le Cren (1958)	8
Rhodeus amarus	European bitterling	0	12	W	2	Konečná et al. (2009)	0
Rutilus rutilus	roach	0	10.2	W	1	Mooij et al. (1994)	1
		0	11.5	W	1	Mooij and van Tongeren (1990)	1
		0	12	W	9	Cowx (2000)	0
		0	12	W	4	Grenouillet et al. (2001)	0
		0	12	W	4	Nunn et al. (2003)	3
		1-5	13	W	3	Müller and Jurg Meng (1986)	0
		0	14	W	3	Broughton and Jones (1978)	0
		0	14	W	9	Griffiths and Kirkwood (1995)	0
		0	16	W	3	Kempe (1962)	0
		0	17.5	W	1	Mooij et al. (1994)	1
Salmo salar	atlantic salmon	1	0[d]	W	9	Jonsson et al. (2005)	0
		unknown	0[d]	W	9	Skinner et al. (2008)	0
Salmo trutta	brown trout	0-1	0[d]	W	8	Baglinière and Maisse (1990)	0
		0	0[d]	W	9	Ojanguren and Braña (2003)	0
Sander canadensis	sauger	1-6	5	W	2	Braaten and Guy (2002)	0
Sander lucioperca	pikeperch	0	10	W	1	Mooij et al. (1994)	2
Sander vitreus	walleye	0	5	A	10	Uphoff et al. (2013)	0
Semotilus atromaculatus	creek chub	0	0	W	9	Schlosser et al. (2000)	0
Squalius cephalus	European chub	0	12	W	2	Mann (1976)	1
		0	12	W	4	Nunn et al. (2003)	2
Thymallus thymallus	grayling	0	0[d]	W	9	Haugen (2000)	1
Multiple species	Multiple species	0-1	12	W	4	Wolter (2007)	0

[a] Age-0 refers to young of the year; all other values are age-classes.

[b] W=water, A=air.

[c] 1=fit a growth model (e.g. bioenergetics model), 2=minimum temperature for physiological process, 3=goodness of fit (e.g. T_o that maximizes r^2), 4=used for common dace (Mills and Mann 1985), 5=used for European perch (Le Cren 1958), 6=commonly used in plant studies, 7=physiologically relevant to *O. mordax,* 8=used for Atlantic salmon (*Salmo salar*) egg survival (Ketola 2000), 9=none given, 10=used in Shuter et al. 1983 among population study.

[d] T_o not reported; assumed to be 0^oC

Table 2.2 Species-specific summary of fish data from both the OMNR and MNDNR. ADD_0 range is the observed range of annual degree-days above 0^oC across all cohorts and waterbodies, and cohorts is the number of unique age classes in a given sampling year summed across all sampling years and waterbodies.

scientific name	common name	waterbodies	ADD_0 range	cohorts	fish
Catostomus commersonii	white sucker	1	2523-3083	6	54
Coregonus artedi	cisco	1	2617-3132	5	135
Esox lucius	northern pike	1	2482-3084	5	113
Lepomis macrochirus	bluegill	2	2584-3637	11	116
Morone chrysops	white bass	1	3153-3863	6	62
Perca flavescens	yellow perch	8	2517-3567	93	3652
Sander canadensis	sauger	6	2295-4110	86	2680
Sander vitreus	walleye	81	1886-4110	976	40674

Table 2.3 Parameter values and range limits for using equation 2.4 to convert annual degree-days at a given T_o ($ADD_{T_{o,x}}$) to annual degree-days at one of four T_o standards ($ADD_{T_{o,y}}$). Parameter values were estimated for each standard T_o by fitting curves to describe how the slope and intercept of the $ADD_{T_{o,y}}|ADD_{T_{o,x}}$ relationship changed with T_o (CurveExpert Professional 1.6.5). Only $ADD_{T_{o,y}}|ADD_{T_{o,x}}$ regressions with an $r^2 > 0.90$ were included when describing these relationships. The $T_{o,x}$ range limit indicates the range of T_o values from which conversion is appropriate and the $ADD_{T_{o,y}}$ range limit indicates the range of ADD values to which conversion is appropriate. Conversion outside of either of these ranges is likely to result in greater prediction error ($ADD_{T_{o,y}}\ \overline{\overline{SE}}$).We estimated prediction error and its standard deviation via bootstrap validation of equation 2.4 ($1\text{x}10^4$ iterations).

Standard T_o (ºC)	Slope parameter values			Intercept parameter values		$T_{o,x}$ range limit (ºC)	$ADD_{T_{o,y}}$ range limit (ºC·days)	$ADD_{T_{o,y}}\ \overline{\overline{SE}}$ and $(\sigma_{\overline{\overline{SE}}})$
	a_1	a_2	a_3	a_4	a_5			
0	0.05	0.99	-	126.00	-32.44	0-8	1809-3725	46 (0.61)
5	1.31	-0.08	0.81	96.04	-446.21	0-12	922-2425	37 (0.32)
10	1.66	-0.05	1.13	68.61	-681.79	2-16	45-1464	26 (0.36)
15	3.77	-0.36	0.75	35.98	-544.76	8-19	43-743	17 (0.24)

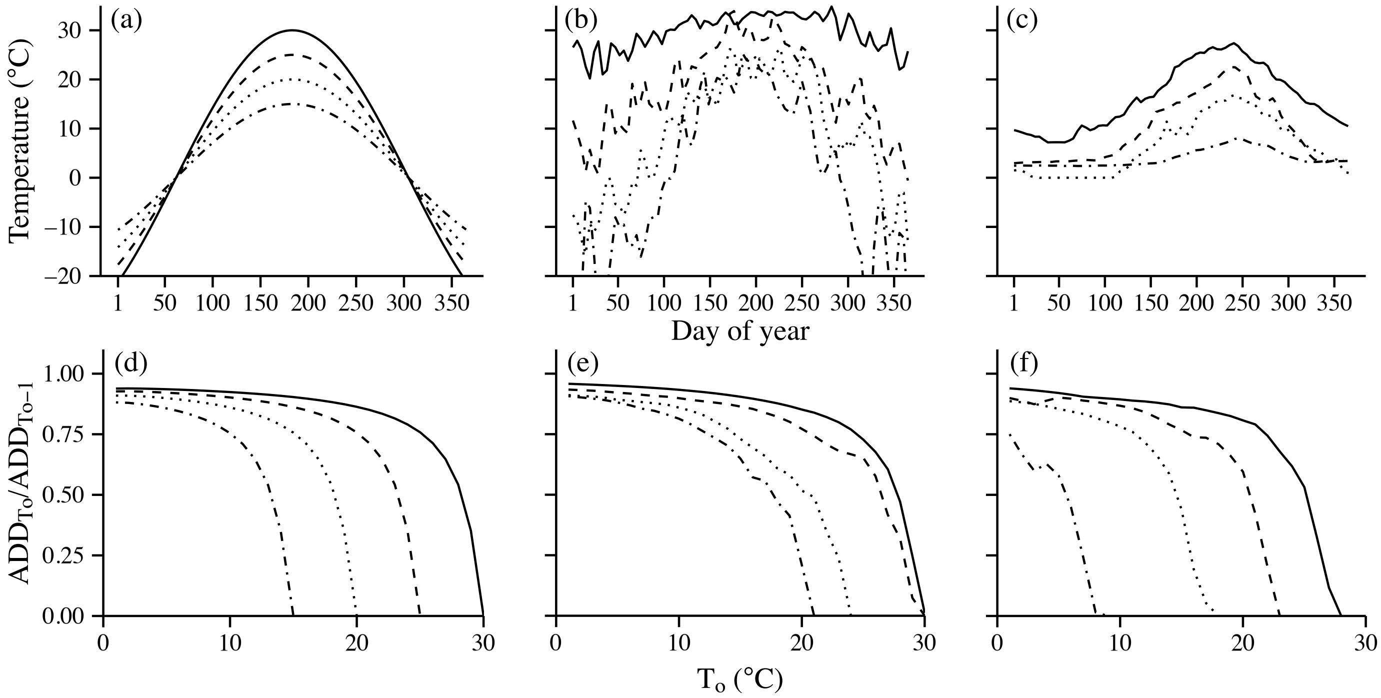

Figure 2.1 Annual temperature curves and associated values of ADD_{To} expressed as a proportion of ADD_{To-1}. Data in (a) and (d) are from a sine curve (equation 2.2) with *w* values of 15 (·-·), 20 (···), 25 (--) and 30°C (-). Data in (b) and (e) are from daily 2009 T_{Min} and T_{Max} values at weather stations (NOAA, unpublished data, National Climatic Data Center) in Bettles Alaska (·-·), Duluth Minnesota (···), Springfield Missouri (--) and Everglade City Florida (-). Data in (c) and (f) are from daily mean temperature values taken above the thermocline within Shadow Bay of Lake Chaeukuktuli Alaska, 2008 (·-·) (Darrell S. Kaufman, unpublished data, Climatic records from lakes in southern Alaska), Lake Superior Minnesota (NOAA, unpublished data, Index of publications and tech reports), 1992 (···), Pillager Lake Minnesota, 2011 (Andrew Carlson MnDNR, unpublished data, 1601 Minnesota Drive, Brainerd, MN 56401) (--) and Lake Powell Utah, 2011 (-) (Wayne Gustaveson, unpublished data, water-data.com).

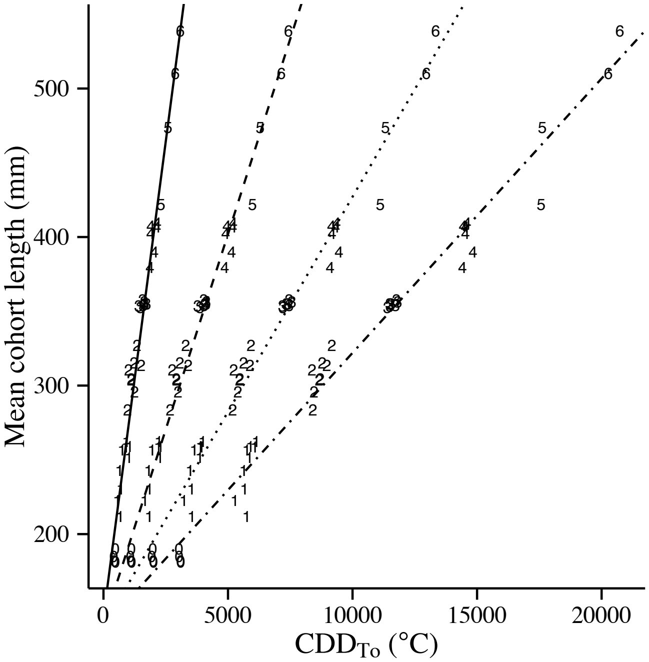

Figure 2.2 Example mean cohort length-at-age given CDD$_{To}$ regression analysis at $T_o = 0$ (·-·), 5 (···),10 (--), and 15ºC (-). Data are from walleye in Cass Lake, MN. Number points show the age in years of each cohort. Each regression had 36 degrees of freedom, p-values<0.05 and r^2 values ≥ 0.97.

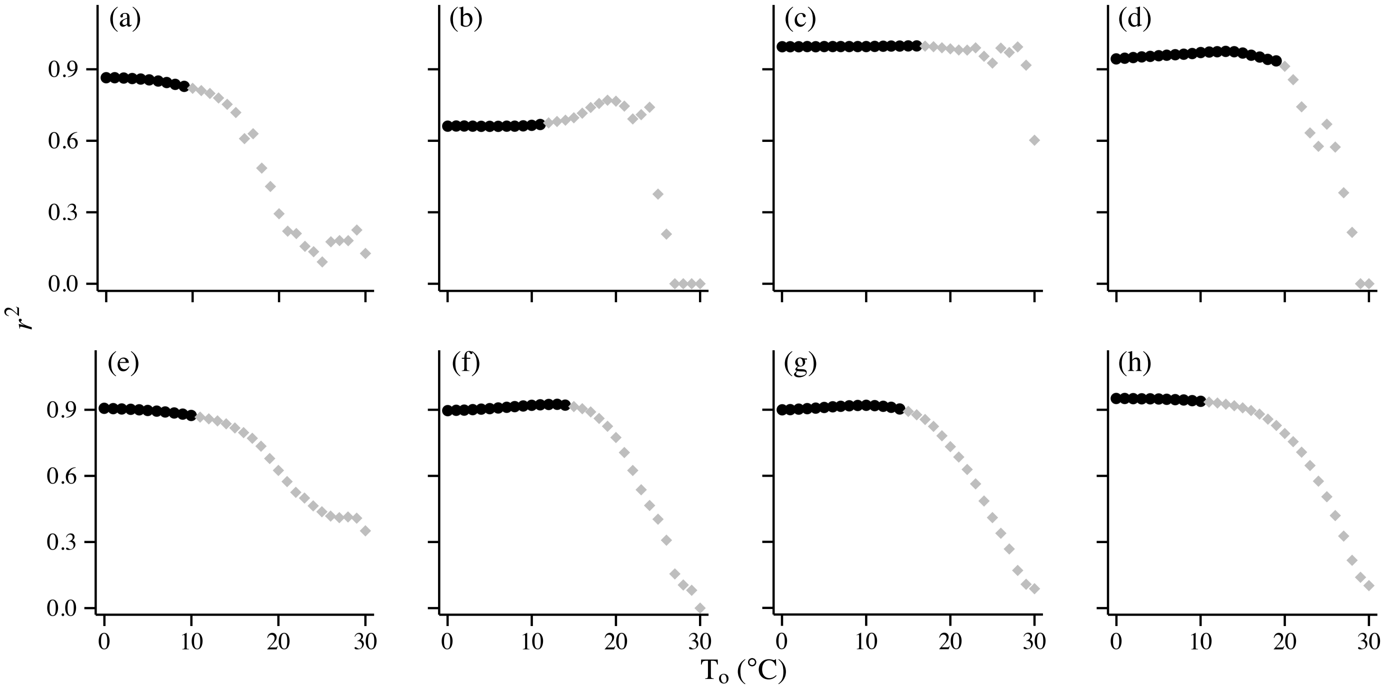

Figure 2.3 The coefficient of determination (r^2) for the relationship between total length (mm) and CDD_{To} over a range of T_o values for (a) white sucker in Lake of the Woods ON (see Table 2.2), (b) cisco in Leech Lake MN (see Table 2.2), (c) northern pike in La Cloche Lake ON (see Table 2.2), (d) bluegill in Pumushe Lake MN (63 individuals across 6 cohorts), (e) white bass in Lac Qui Parle MN (see Table 2.2), (f) yellow perch in Lake Mille Lacs MN (2299, 26), (g) sauger in Lake Pepin MN (859, 21) and (h) walleye in Lake Pepin MN (616, 26). Filled circles show the approximate extent of each r^2 plateau.

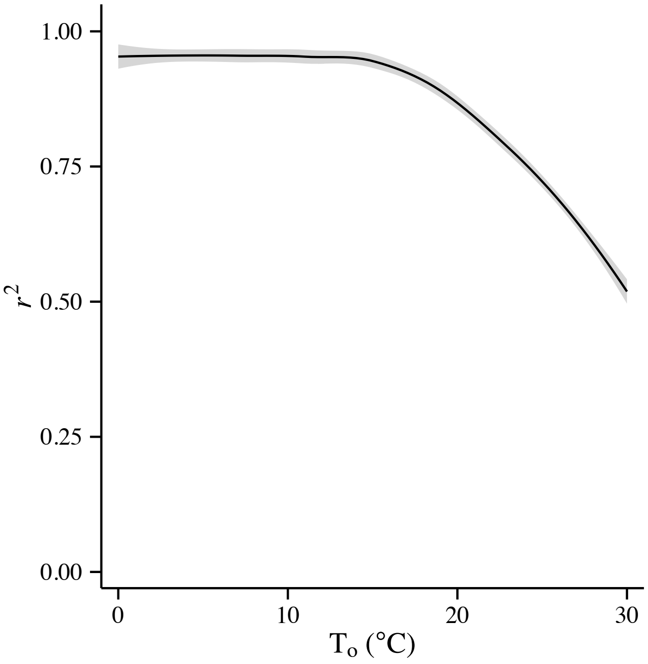

Figure 2.4 The coefficient of determination (r^2) for the relationship between total length (mm) and CDD_{To} over a range of T_o values, averaged over 81 walleye populations in Minnesota (*n*=20) and Ontario (*n*=61). The solid line is LOESS fit ($\alpha = 0.65$) of all data combined and the shaded area is the 95% confidence interval.

Chapter 3

Fish growth and degree-days II: Selecting a base temperature for an among population study.

Synopsis

The degree-day (DD) is a method of describing the thermal opportunity for growth and development in fish, and is becoming increasingly popular when comparing growth over large spatial scales. The degree-day equation includes a lower temperature threshold (T_o) so that calculations are constrained to temperatures that are relevant to growth. However, there is currently no convention for choosing T_o, and unknown are the effects of an incorrect T_o on how growth is perceived. We used model simulations to demonstrate an effect of T_o error on apparent growth that increased both with the size of the error and the among-population difference in thermal habitat. We then showed the same relationships in an analysis of length-at-age data from 81 walleye (*Sander vitreus*) populations in North America. Our results show that apparent differences in among-population growth can be an artifact of T_o rather than a significant biological phenomenon, especially when populations span a wide thermal range. To minimize this artifact, we recommend carefully assigning species to one of four T_o standards (0, 5, 10, 15^{o}C).

3.1 Introduction

The relationship between fish growth and temperature is well documented and highly correlated (Brett 1969, Fry 1971) yet many growth models do not incorporate a thermal component (Neuheimer and Taggart 2007). The degree-day (DD_{To}; ^{o}C·days) is an index of the thermal opportunity for growth and development. Degree-day calculations incorporate a lower threshold temperature (T_o) so that they are limited to temperatures relevant to growth. However, Chezik et al. (*in review*) showed that precise T_o estimates are largely unnecessary when explaining annual growth in a single population because degree-days at different T_o values tend to be similar (especially as T_o approaches 0^{o}C).

Although T_o matters little when describing growth in a single population, T_o may become important when describing growth over a wide thermal range. For example, we can imagine a simple thought experiment in which growth rates at the thermal extremes of a species' range are identical, but can appear to be different depending on T_o (Fig. 3.1). We begin by imagining separate annual temperature curves that describe the thermal environment at these extremes. We also imagine that fish at these extremes share a growth rate $\left(\frac{mm}{°C \cdot Day}\right)$ and do not grow below some limiting temperature (i.e., 'true' T_o). If we calculate degree-days at 'true' T_o, fish at either extreme have identical growth rates. However, if we calculate degree-days assuming a T_o above 'true' T_o, fish in the cooler environment appear to be growing faster (i.e., $\frac{mm}{°C \cdot Day}$ is greater).

In our thought experiment, the apparent difference in growth rate at $T_o >$'true' T_o stems from differences between the annual temperature curves of the cooler and warmer environments. In both environments, 'true' degree-days are underestimated at high T_o because degree-days decrease with increasing T_o. As the number of degree-days decrease, apparent growth rates $\left(\frac{mm}{°C \cdot Day}\right)$ increase because growth remains constant. However, this effect is exaggerated in the cooler environment because degree-days in cooler environments decrease with increasing T_o more rapidly than in warmer environments (Fig. 3.1e). Therefore, because T_o in our thought experiment is > 'true' T_o, fish in the cooler environment appear to grow faster than fish in the warmer environment.

This thought experiment suggests that T_o can influence our interpretation of growth rates among populations that are thermally dissimilar.

If T_o can exaggerate differences in apparent growth rates among populations then this may have implications for studies that use degree-days to describe and compare growth over a wide thermal range (Table 3.1). For example, many species exhibit counter-gradient growth, which is an increase in growth rate with latitude (e.g., Power and McKinley 1997, Conover et al. 2009, Chavarie et al. 2010). This pattern has been attributed to genetically based phenotypic adaptations to climate (Rypel 2012) but it could also be a statistical artifact that resulted from an inappropriate T_o. Current methods for identifying T_o do not consider and have not accounted for the effect of T_o on apparent growth. In fact, many studies provide little or no justification for their use of T_o and when justification is provided, it is usually that T_o is the approximate minimum temperature associated with some physiological process (e.g., growth). These various methods have resulted in a wide range of T_o values (0-18ºC) currently in use among species, with as many as four different values applied to a single species (e.g., yellow perch, *Perca flavescens,* 0, 5, 10 and 13.5ºC) (Table 3.1).

In this study, we determine the effect of T_o on apparent growth rates among populations in thermally dissimilar environments. This work is a companion to Chezik et al. (*in review*), which describes how degree-days vary with T_o, and how this variation affects the ability of degree-days to account for growth in a single population. Here we explore how the relationship between degree-days and T_o varies among waterbodies in different climates, and determine how this variation affects differences in apparent growth. We explore these relationships by using both theoretical and empirical data to compare among-population growth rates across thermal ranges and for different values of T_o.

3.2 Simulated effects of T_o and thermal difference on apparent growth rates

In this section, we simulate the thought experiment in Fig. 3.1 using hypothetical data from four populations; we then simulate an extensive database to determine how apparent growth rates might vary both with T_o and the degree of thermal difference among populations. The populations in these simulations share i) a maximum annual air temperature of 35ºC, ii) a growing season of 160 days, iii) an immature growth rate of 0.03 $\frac{mm}{°C \cdot Day}$ at a T_o of 5ºC, and iv) no discernable length at hatch. This approach ignored interactions between growing season, mean annual temperature and maximum annual temperature in favor of a simplified model for exploring how among-population differences in the availability of thermal energy affect apparent growth. We used a sine curve (Arnold 1959) to generate annual temperature profiles for each simulated waterbody and then calculated annual degree-days (ADD_{To}; $^oC \cdot$days) by integrating the area under each curve (Baskerville and Emin 1969, Chezik et al. *in review*). Temperature curves and ADD_{To} values varied by their assigned mean annual temperature determined in each simulation. We then predicted immature length-at-age as

$$\hat{L} = \frac{dl}{dDD_5} \cdot [(ADD_5 \cdot Age) + ADD_5], \tag{3.1}$$

where, $\frac{dl}{dDD_5}$ is the change in length per degree-day at a T_o of 5ºC, *Age* is age in years assuming a common birthday of January 1, and ADD_5 is the annual degree-days experienced at a T_o of 5ºC. In this way each simulation was made up of thermally unique waterbodies with fish that share a common growth rate.

To simulate the effect of T_o on apparent immature growth, we imagined three studies that compared growth in four waterbodies over a large thermal range. These four waterbodies had mean annual temperatures of -7, 5, 17, and 29ºC, respectively. The three studies were identical except that each used a different T_o to calculate degree-days (-5, 5, and 15 ºC). Our simulation showed that the study that assumed a T_o of 5ºC would have concluded that all populations shared the same growth rate, but that the other studies would have concluded that growth rates either increased (T_o = 15ºC) or decreased (T_o = -5ºC) over the same thermal range (Fig. 3.2). Because growth in our simulation began at 5ºC (i.e., 'true' T_o = 5ºC), apparent differences in immature growth were entirely an artifact of choosing an inappropriate T_o. As in our simple thought experiment, these artifacts stem from the interaction between an inappropriate T_o and among-waterbody differences in annual temperature curves. Specifically, an inappropriate T_o biases degree-day calculations in all waterbodies, but this bias is smallest in the warmest waterbody and largest in the coolest waterbody. These degree-day differences translate into apparent differences in the rate at which fish grow in different thermal environments.

Given that apparent growth rates depend on T_o and among-waterbody differences in annual temperature (Fig. 3.2), it stands to reason that the effect of an inappropriate T_o on apparent immature growth increases with both the among-waterbody difference in annual temperature and the difference between ‘inappropriate’ T_o and ‘true’ T_o. To test these hypotheses, we first created 200 waterbodies with mean annual temperatures that were uniformly spread over a narrow thermal range (7.3-7.9ºC). Each temperature curve was approximated by a sine curve (Baskerville and Emin 1969, Chezik et al. *in review*) and ADD values were calculated for each T_o in the range -20 to 20ºC. We used equation 3.1 to generate immature length-at-age data for each temperature curve (i.e., waterbody) and we incorporated temperature-independent variation in length-at-age by randomly sampling normal distributions centered on each calculated length-at-age, assuming a standard deviation of 0.08 mm. This standard deviation was based on observed variation in walleye length-at-age (see next section) and was therefore realistic. We incorporated temperature independent length-at-age variation because growth is rarely exclusively dependent on temperature in natural systems.

For each waterbody, we estimated immature growth rate by regressing length onto cumulative degree-days (CDD; $^{o}C{\cdot}days$) (i.e., the summation of all experienced ADD_{To}) at each T_o value. We then identified the T_o that minimized the coefficient of variation (CV) in growth rates among waterbodies. Our rational for using the CV was that, whereas growth rates at ‘true’ T_o are identical in deterministic simulations (Fig. 3.2), growth rates at ‘true’ T_o are likely to be most similar in stochastic simulations. However, because variation in length-at-age can result in the CV being minimized at a T_o other than ‘true’ T_o, we allowed the CV method to identify biologically meaningless (i.e., negative) T_o values (Yang et al. 1995, Legg 1998a). To determine the distribution of T_o values at which CV was likely to be minimized, we generated length-at-age data 1000 times for each waterbody, and for each iteration determined the T_o at which CV was minimized. We then repeated this entire process for 200 waterbodies that had mean annual temperatures spread uniformly between 0 and 15ºC. The result was two distributions of

T_o values at which the CV of growth was minimized, one for a wide thermal range and one for a narrow thermal range.

These preliminary simulations show that, on average, CV was minimized when T_o was equal to 'true' T_o (Fig. 3.3a). This relationship was especially pronounced for the large thermal range. The large thermal range also resulted in a much narrower distribution of T_o values over which CV was minimized (Fig. 3.3b). This inverse relationship between thermal range and the width of the T_o distribution resulted from the relative importance of among-waterbody thermal variation and variation in length-at-age. When waterbodies were distributed over a small thermal range, among-waterbody variation in growth was primarily a result of variation in length-at-age (i.e., noise) such that the CV was minimized over a wide range of T_o values. When waterbodies were distributed over a large thermal range, among–waterbody variation in growth was primarily a result of differences in mean annual temperature such that the CV was minimized at only a few T_o values.

Finally, we created 38 additional thermal ranges that had a median annual temperature of 7.5ºC and were uniformly distributed in width between the narrowest thermal range (7.3-7.9ºC) and the widest thermal range (0-15ºC). As described above, each thermal range contained 200 waterbodies and length-at-age in each waterbody was randomly generated 1000 times. When growth was simulated in this way, we found that as thermal range increased, there was a rapid decrease in the distribution of T_o values at which CV was minimized (Fig. 3.4a) and gradual increase in the effect of T_o on apparent growth (Fig. 3.4b). Figure 3.4b shows clearly that increased differences in growth rates over a wide thermal range are a result of a bias that was introduced by selecting an inappropriate T_o. This bias increased with the magnitude of the difference between inappropriate T_o and 'true' T_o. The results of this simulation suggest that evidence for counter-gradient growth among populations can be a result of T_o rather than a biological phenomenon. For instance, in this simulation, using a T_o of 15 rather than the 'true' value of 5ºC inflated growth rates by 5% over a thermal range of 900 ºC·days.

3.3 Observed effects of T_o and thermal difference on apparent growth rates

Although our simulations show that an inappropriate T_o can artificially generate among–waterbody differences in growth rate, especially over large thermal ranges, unknown is the extent to which this effect is observable in nature. To determine if among-waterbody variation in observed growth is sensitive to T_o and thermal range, we analyzed a database of immature walleye (*Sander vitreus*) length-at-age (40,674 individual records) and air temperature data from 81 waterbodies throughout Minnesota, US, and Ontario, Can. See Chezik et al. (*in review*) for a detailed description of this database. In brief, individual fish records were collected by the Minnesota Department of Natural Resources (2001-2011) and the Ontario Ministry of Natural Resources (1993-2008). Fish records included, waterbody, sample date (day, month, year), age (years), total length (L; mm) and maturity. For waterbodies in Minnesota, air temperature data (T_{Max} and T_{Min}) were kriging-interpolated onto 100km^2 grids and temperatures estimated by determining the grid point nearest the centroid of each lake. Degree-days were calculated at a range of T_o (0-20ºC) and summed to produce annual degree-days (ADD_{To}) for each year of interest. For waterbodies in Ontario, ADD_{To} values were obtained using the Historic Climate Analysis Tool (Cross et al. 2012). We assigned CDD_{To} values to each fish by summing the annual degree-days experienced prior to capture.

Our analysis of observed length-at-age data was similar to our analysis of simulated length-at-age data. For each waterbody, we regressed mean length-at-age onto cumulative degree-days at each T_o in the range 0-20ºC and determined growth rate ($\frac{mm}{°C\cdot day}$) using ordinary least squares. We used a simple linear model because linear immature growth is predicted by theory (Quince et al. 2008) and was observed in this database (Chezik et al. *in review*). We then defined 17 unique thermal ranges, each containing ≥15 waterbodies. To define these thermal ranges, we first determined the thermal character of each waterbody by i) identifying all unique years experienced by the cohorts in a given waterbody, and ii) calculating mean ADD_0 across these years. We then identified the 15 waterbodies that had mean ADD_0 values that were closest to the median ADD_0 (2645 °C·days) across all waterbodies in the database. This step established a narrow thermal range (2550-2720 °C·days) that included a 'thermal group' of 15 waterbodies. We began with 15 waterbodies to ensure a large enough sample to meet the needs of all statistical methods (see next paragraph). We then increased the thermal limits of the initial range in increments of 100°C·days. Additional thermal groups were identified as the number of included waterbodies increased. This process resulted in 17 thermal ranges, the largest of which ranged from 2090-3710 °C·days at T_o of 0ºC and included all waterbodies. For each thermal range, we generated a distribution of T_o values at which the CV of growth was minimized by sampling, without replacement, 85% of waterbodies 1000 times. This approach assumed that sample variance was approximately equal to 'population' variance. This procedure was nearly identical to that of our simulation in the previous section, except the number of waterbodies (i.e., growth rates) in each thermal group was variable and waterbodies were unevenly distributed over the thermal range.

Our results show that the CV in growth rate among waterbodies increased with T_o (Fig. 3.5a). This effect was more pronounced over the entire thermal range than it was over the narrowest thermal range (Fig. 3.5a). The distribution of T_o over the entire thermal range had a median value of 3ºC with a range of 0 to 6ºC (Fig. 3.5b). Over the narrowest thermal range the median value of T_o was 0ºC (range 0 to 16ºC). Furthermore, as thermal range decreased, CV in growth tended to be minimized at a T_o of 0ºC (Fig. 3.5b). This trend was a result of limiting our empirical statistical analysis to biologically relevant (i.e., non-negative) T_o values. As noted in Yang et al. (1995) T_o identification using statistical analysis may sometimes select negative values that make little biological sense. This limitation resulted in a standard deviation of 0 for many thermal groups (Fig. 3.6a). A result more similar to figure 3.4a is expected if negative values were included. Finally, when using a T_o of 15ºC, the difference in growth rate between the 1st and 3rd quartiles significantly increased with thermal range (Fig. 3.6b). The difference in the growth rate interquartile range was as much as $0.12\,\frac{mm}{°\mathrm{C}\cdot\mathrm{day}}$ higher than the smallest thermal group. We did not detect a significant effect of T_o on apparent growth rates when T_o was 0, 5, or 10ºC.

3.4 Discussion

Our results show that apparent growth rates vary with both T_o and thermal range (Fig. 3.4), and that these relationships are observable in empirical data (Fig. 3.6). The apparent variability in growth rate increases as assumed T_o deviates from the T_o that minimizes the among-waterbody variation in growth rate (presumably 'true' T_o), and this effect becomes more pronounced as the thermal range among waterbodies increases (Fig. 3.4b). For instance, we found that variation in the growth rates of immature walleye increased with thermal range when T_o was 15ºC, but not when T_o was 0, 5, or 10ºC. This result suggests that a hypothetical study that used a T_o of 15ºC to compare growth rates among the populations in this database would have concluded that walleye are latitudinally adapted and exhibit counter-gradient growth. Given the results of our simulation (Fig. 3.4b) and the absence of counter-gradient growth at lower values of T_o (Fig. 3.6b), it is entirely possible that this conclusion would be false. Overall, our analyses suggest that it is possible to falsely detect counter-gradient growth, and that care must be taken to select a T_o that minimizes this statistical bias.

The effect of assumed T_o on apparent growth rates is greater when assumed T_o is less than 'true' T_o than when assumed T_o is greater than 'true' T_o (Fig. 3.3a, Fig. 3.5a). In our simulations, the effect of T_o on apparent growth stemmed from both error in T_o and among-waterbody differences in temperature curves. When both of these conditions were met they resulted in waterbody-specific biases in apparent growth. However, because annual degree-days become more similar as T_o values get smaller (Chezik et al. (*in review*), biases in degree-days, and therefore the bias in apparent growth, were larger when T_o was overestimated by some amount than when T_o was underestimated by the same amount.

Given that the effect of assumed T_o on apparent growth rates is greater when assumed T_o is larger than 'true' T_o, a risk-averse strategy is to err low when selecting a T_o for an among-population study. This will reduce the risk of introducing bias that may otherwise result when simply relying on precedent or convention. For example, Power and van den Heuvel (1999) compared the growth of yellow perch in northern Alberta to a population in southern Manitoba using a T_o of 13.5ºC. This T_o is routinely used to describe European perch (*P. fluviatilis*) growth in Lake Windermere (Le Cren 1958), but may be sufficiently high to introduce a bias when comparing growth over a wide thermal range (ΔADD5 ~950 °C·days). To test for such a bias, we repeated the Power and van den Heuvel (1999) analysis for a range of T_o values (5-12ºC and 13.5ºC). Our results (Table 3.2) show that the difference between growth models (i.e., growth rates) is greatest at 13.5ºC and statistically insignificant when T_o is 8, 9 or 10ºC (Fig. 3.7). Power and van den Heuvel (1999) attributed the evidence for counter-gradient growth at T_o = 13.5ºC to "latitudinal or trophic factors"; however, our re-analysis suggests that this evidence is either exaggerated or solely a result of an inappropriately large T_o. Although this study may be an example of T_o detecting growth differences when none exist, it is encouraging that many comparative growth studies tend to use low values of T_o that are less prone to artificially inflating growth rates (Table 3.1). However, we suspect that 18ºC (the minimum temperature for growth of larval gar, *Lepisosteus oculatus*) is too high for comparing growth of individuals age 0-16 over 2240-7570 ADD_5 (David 2012).

If error in T_o can bias among-population growth studies, especially over wide thermal ranges, it follows that T_o should be estimated with care. Unfortunately, many T_o values currently in use are rarely justified (Table 3.1) and others may bias results (e.g., Power and van den Heuval 1999). Our results suggest that T_o can be estimated as the T_o that minimizes the CV of growth over a large thermal range; however, data are rarely available to perform such an analysis. Similarly, although there are methods for estimating T_o in single populations, results often vary among methods and populations (reviewed by Chezik et al. *in review*).

A relatively simple approach of estimating T_o is to determine the mean development temperature and subtract 10ºC (Charnov and Gillooly 2003). To demonstrate, we used the Wisconsin Bioenergetics model (Hanson et al. 1997) to describe how walleye and yellow perch growth rates changed with temperature (Fig. 3.8). Given that mean developmental temperature in these species occurs at 15 and 18ºC, respectively, the "10ºC rule" predicts that T_o is 5 and 8ºC, respectively. These results are consistent with our analysis of walleye data (i.e., 3ºC, Fig. 3.5b), and with our re-analysis of yellow perch data showing that among-population variation in perch growth was minimized at 9ºC. Although the method needs to be explored further, it does show promise as a means of assigning a species to one of the T_o standards (0, 5, 10, and 15ºC) advocated by Chezik et al. (*in review*). Assigning species to a standard T_o (e.g., 5ºC for walleye and 10ºC for yellow perch) would minimize the risk of using T_o values that bias growth rate comparisons, simplify comparisons among datasets and studies, and facilitate the use of degree-days in future studies.

In this study, we have shown that an inappropriate T_o can bias growth comparisons among waterbodies. This bias leads to apparent differences in growth rates among populations that are solely an artifact of T_o. This effect of T_o on apparent growth is exaggerated by large thermal differences among waterbodies. Because these thermal differences are predominately observed over a latitudinal gradient, an inappropriate T_o can result in the appearance of counter-gradient growth. To minimize the risk of introduced bias, we suggest first estimating T_o using the "10^{o}C rule" (Charnov and Gillooly 2003) method and then setting T_o to the nearest standard value. Doing so will limit the introduction of a bias that may obscure differences among populations and both simplify and encourage the use of degree-days in future studies. Although, there is no evidence that this effect of T_o is observed in marine systems, until further study we suggest taking similar precautions when choosing T_o. The results of this study should pertain to spatially isolated marine populations that inhabit thermally dissimilar environments. Populations that are not geographically isolated and therefore can behaviorally thermo-regulate, are unlikely to exhibit an affect of T_o on apparent growth rates.

Table 3.1 A summary of published T_o values used in comparative growth studies of freshwater fishes over a thermal gradient (i.e., ADD_5 range).

scientific name	common name	location(s)	T_o (°C)[a]	temperature medium	justification[b]	ADD_5 range (°C·days)	reference
Acipenser fluvescens	lake sturgeon	Canada (MB, ON, QC, SK), US (WI)	5	A	1	650-2250	Power & McKinley (1997)
Esox lucius	northern pike	Minnesota	10	A	2	550-4010[d]	Jacobson (1992)
		North America & Eurasia	10	A	3	1120-2730[e]	Rypel (2012b)
Ictalurus punctatus	channel catfish	Illinois	10	A	2	4080-6080[d]	Shoup et al. (2007)
Lepisosteus oculatus	spotted gar	US (AL, AR, IL, KY, LA, MI, MS, TX)	18	A	1	2240-7570[f]	David (2012)
Lepomis macrochirus	bluegill sunfish	Illinois	10	A	2	4080-6080[d]	Shoup et al. (2007)
Micropterus dolomieu	smallmouth bass	Canada & US	10	A	4	1160-4660[d]	Beamesderfer & North (1995)
		Canada & US	10	A	4	1640-3950[e]	Dunlop & Shuter (2006)
Micropterus salmoides	largemouth bass	Canada & US	10	A	4	1160-4660[d]	Beamesderfer & North (1995)
		Illinois	10	A	2	4080-6080[d]	Shoup et al. (2007)
		Canada & US	10	A	5	1030-7510[f]	McCauley & Kilgour (1990)
Morone saxatilis	striped bass	E. USA & E. Canada	10	A	3	1400-5420[d]	Rypel (2012a)
Oncorhynchus clarkii	cutthroat trout	North Central Colorado	0[c]	A	2	900-1010[d]	Coleman & Fausch (2007b)
Perca flavescens	yellow perch	Alberta	0[c]	W	2	1020-1120[d]	Abbey & Mackay (1991)
		Ontario	10	A	1	1030-2330[d]	Chong (2000)
		Ontario	0[c]	W	2	660-1910[d]	Post & McQueen (1994)
		Alberta, Manitoba & Saskatchewan	13.5	W	6	1050-1710	Power & van den Heuvel (1999)
		Ontario	5	A	2	1160-2070	Purchase et al. (2005)
		Ontario	5	W	7	1160-2070	Rennie et al. (2010)
Phoxinus phoxinus	Eurasian minnow	Southern England & Central Finland	5	A	3	470-710	Mills (1988)
Pomoxis nigromaculatus	black crappie	Southern Minnesota	15.5	A	8	2630-3500[f]	McInerny & Cross (1999)
Richardsonius balteatus	redside shiner	Utah, Idaho, Wyoming	8	A	1	1670-3400[d]	Houston & Belk (2006)
Salvelinus alpinus	arctic char	Canada & NE US	0	A	1	30-1960[e]	Chavarie et al (2010)
Sander vitreus	walleye	Canada & US	5	A	2	970-5680[d]	Colby & Nepszy (1981)
		Canada & US	5	A	2	1000-4500	Bozek et al. (2011)
		Wisconsin	0	A	8	1140-1920[d]	Sass & Kitchell (2005)
		Ontario & Quebec	5	A	1	1200-2300	Venturelli at al. (2010)
Multiple species	Multiple species	Michigan	10	A	3	1420-3120[e]	Wagner et al. (2007)

Table 3.1 Continued (footer)

[a] W=water, A=air.

[b] 1=minimum temperature for physiological process, 2=none given, 3=commonly used in plant studies, 4=cites McCauley & Kilgour, 5=fit a growth model (e.g. bioenergetics model), 6=used for European perch (Le Cren 1958), 7=cites Purchase et al. (2005), 8=used for Atlantic salmon (*Salmo salar*) egg survival (Ketola 2000).

[c] T_o not reported; assumed to be 0^oC.

[d] ADD_5 estimated using equation 5 in Chezik et al. (*in review*).

[e] Not given in original literature. Estimated using the 1971-2000 climate normal from the most northern and southern location. Normals were collected from the National Climate Data and Information Archive distributed by Environment Canada and the NOAA National Climatic Data Center.

[f] ADD_5 estimated using equation 5 in Chezik et al. (*in review*) beyond the T_o limit for conversion to T_5.

Table 3.2 Length|CDD_{To} coefficient estimates for three north Alberta lakes (N. Alberta, df=17) and West Blue lake (WBL, df=28) with their associated r^2 values and Chow Test *F*-statistic (F=2,α =0.05) comparing model estimates. All coefficients were significant at an alpha of 0.05.

T_o	*F-statistic*	*a* N. Alberta (mm)	*b* N. Alberta (mm/DD_{To})	r^2 N. Alberta	*a* WBL (mm)	*b* WBL (mm/DD_{To})	r^2 WBL
5	2.624	7.478	0.034	0.962	2.871	0.041	0.951
6	2.367	7.999	0.037	0.961	3.592	0.044	0.952
7	2.087	8.493	0.041	0.960	4.430	0.047	0.954
8	1.782	8.905	0.045	0.960	5.416	0.051	0.955
9	1.567	9.274	0.050	0.960	6.591	0.056	0.957
10	1.749	9.643	0.055	0.960	8.018	0.062	0.959
11	2.932	9.979	0.063	0.959	9.750	0.070	0.962
12	5.156	10.332	0.072	0.956	11.553	0.079	0.965
13.5	7.349	11.199	0.090	0.949	13.648	0.099	0.970

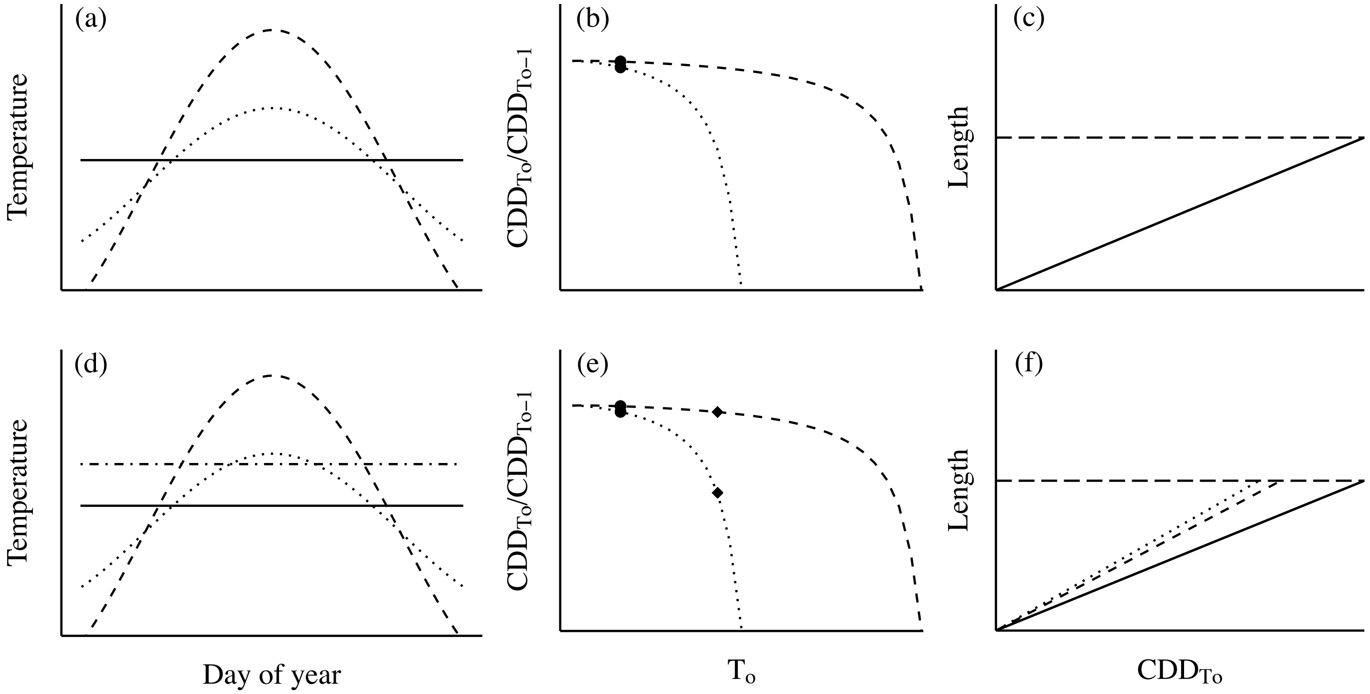

Figure 3.1 Depiction of a hypothetical thought experiment showing the effect of T_o on apparent growth rates in two waterbodies from different climates. Panel (a) is the temperature curves for the two waterbodies: one in a cooler climate (•••) and one in a warmer climate (--). The horizontal line in *a* (-) refers to the 'true' base temperature (T_o) below which fish in these waterbodies do not grow. Panel (b) shows the proportion of cumulative degree-days (CDD; $^oC{\cdot}days$) retained at a given T_o relative to the cumulative degree-days at the previous T_o for both the cool (•••) and warm (--) waterbodies (Chezik et al. *in review*). The (•) shows CDD at 'true' T_o. Panel (c) is the apparent growth trajectory of immature fish in these lakes up to a hypothetical length at maturity (long --) as described by cumulative degree-days at 'true' T_o. Panel (d) depicts the use of an 'incorrect' T_o (•-•) that is higher than the 'true' T_o. Panel (e) shows the proportion of CDD retained at the incorrect T_o (◆) for each waterbody and panel (f) shows the resulting apparent growth rates when using the 'incorrect' T_o. When CDD are calculated using 'true' T_o, immature growth rate is the same for both waterbodies (-). When CDD are calculated using an 'incorrect' T_o, it introduces an error in CDD that is larger in the cool waterbody than it is in the warmer waterbody; as a result, immature growth rate in the cool waterbody (•••) appears to be higher than immature growth rate in the warm waterbody (short --).

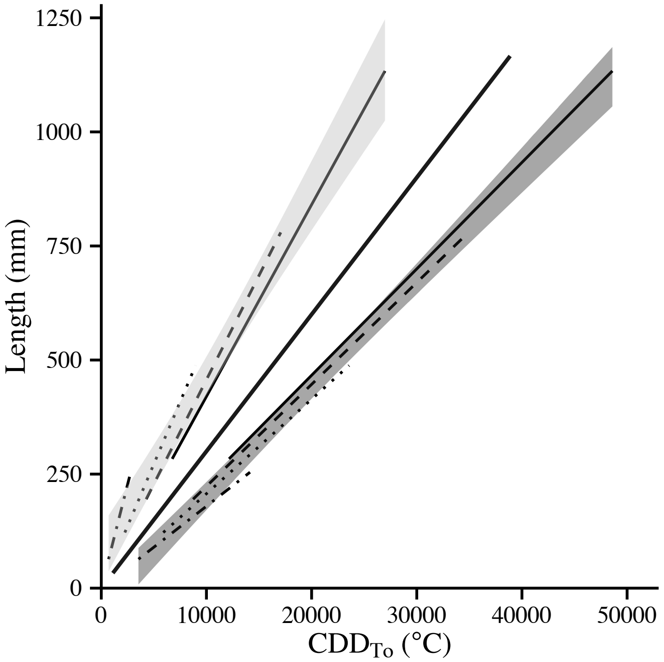

Figure 3.2 Relationship between length and cumulative degree-days at T_o values of -5 (dark grey), 5 (solid line), and 15ºC (light grey) for four hypothetical waterbodies with mean annual temperatures of -7(•-•), 5(•••), 17(--), and 29ºC(-). At T_5 ('true' T_o), all 'populations' share the same slope (i.e., apparent growth rate). At T_{-5} and T_{15}, each 'population' has a unique slope. Populations appear to grow more quickly when assumed T_o is > 'true' T_o, and more slowly when assumed T_o < 'true' T_o. These biases are smallest in the warmest waterbody and largest in the coldest waterbody.

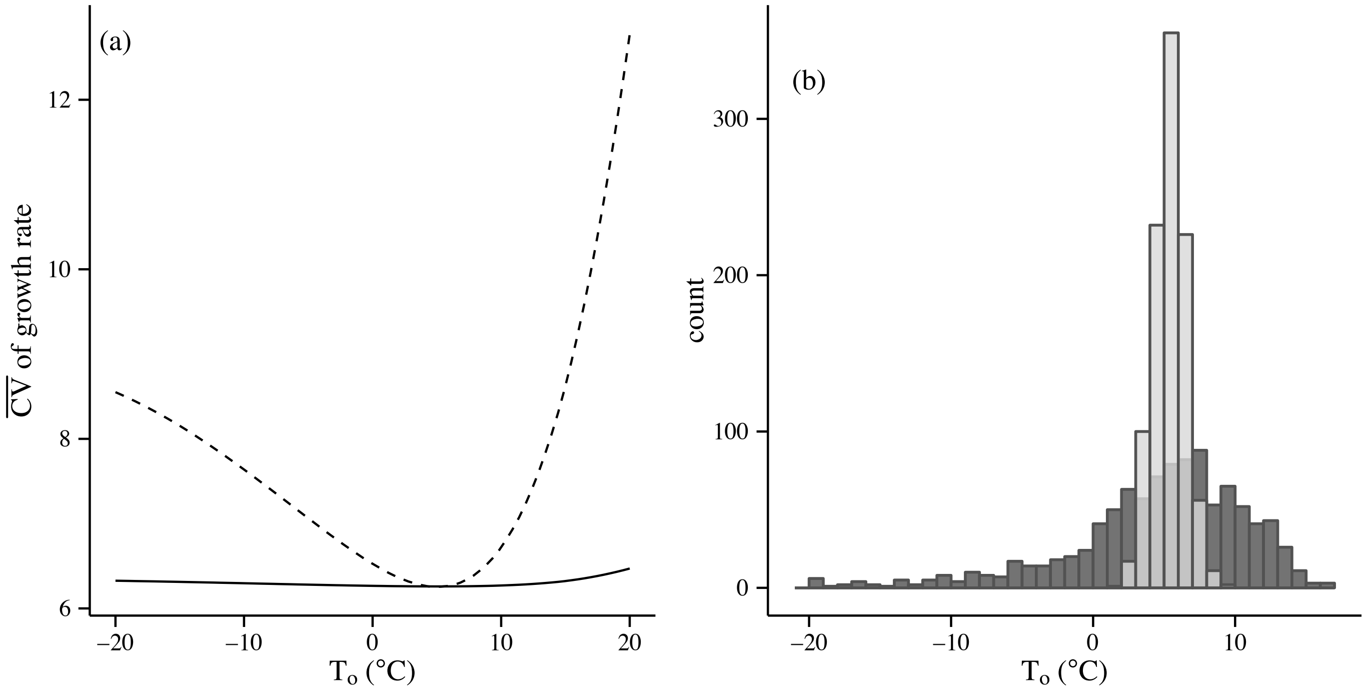

Figure 3.3 Results of 1000 T_o identification simulations over a small thermal range (7.3-7.9ºC, ΔADD_5=180, [--]) and a large thermal range (0-15ºC, ΔADD_5=1150, [-]). Panel (a) shows the mean among-waterbody coefficient of variation in apparent growth rate at each T_o over both thermal ranges. Panel (b) shows the distribution of T_o at which the CV of growth was minimized for both thermal ranges (dark grey, small thermal range and light grey bars, large thermal range, respectively).

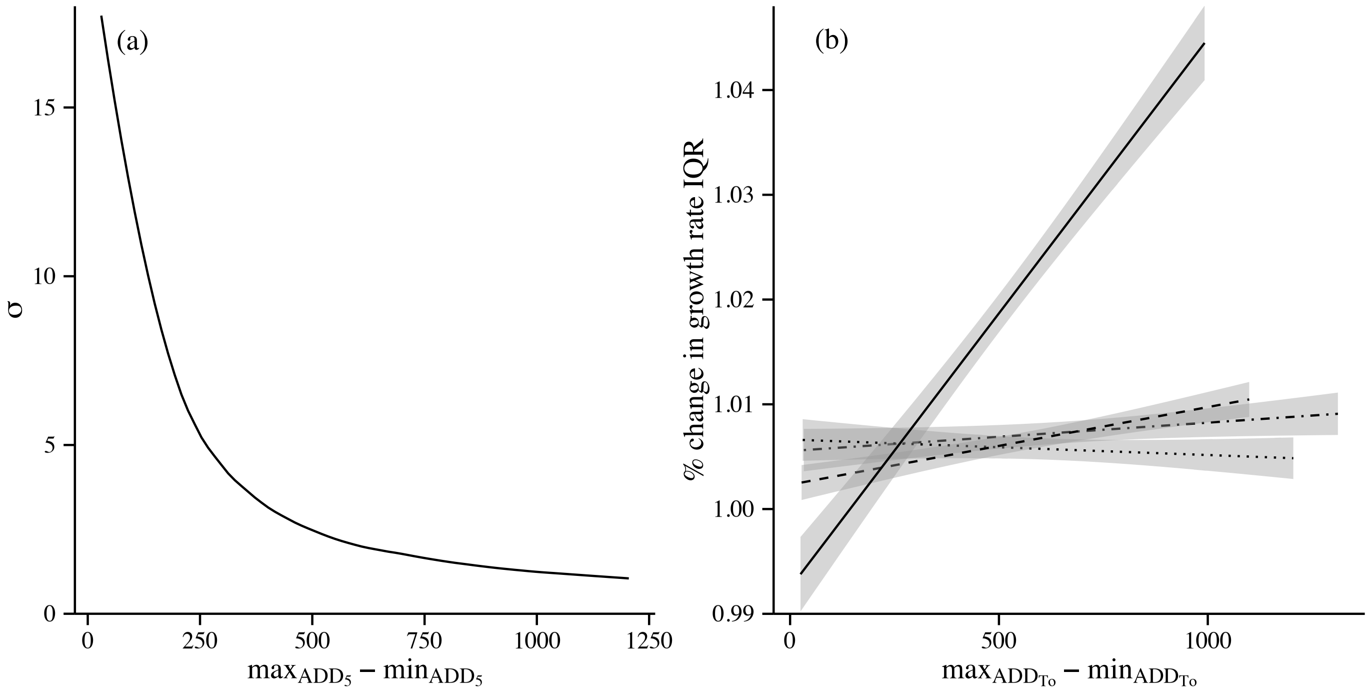

Figure 3.4 Simulation results along a continuum of thermal ranges. Panel (a) shows how the standard deviation (σ) of 1000 T_o estimates change with increasing thermal range. Thermal range is described by ADD values at a T_o of 5ºC but results were the same for all T_o. Panel (b) shows how the growth rate interquartile range (IQR) changes with increasing thermal range when using T_o values of 0 (•-•), 5 (•••), 10 (---) and 15ºC (-). Shaded areas are 95% confidence intervals.

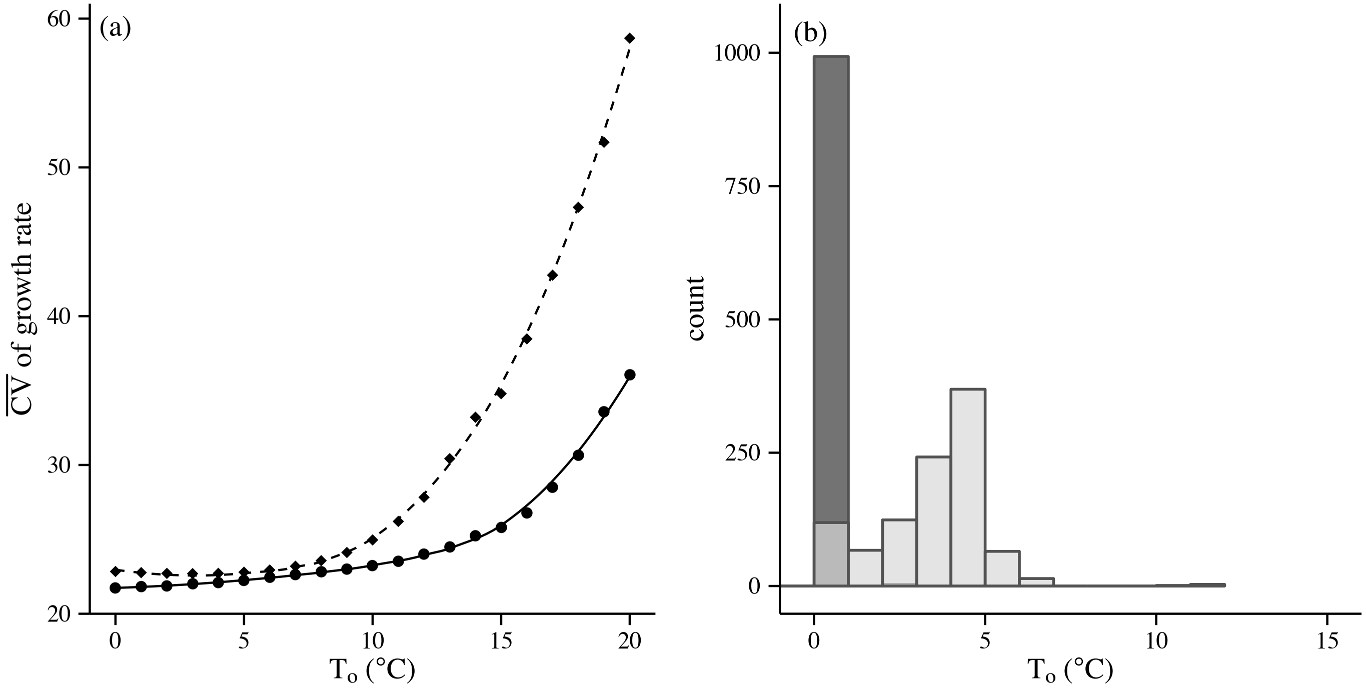

Figure 3.5 Results for 1000 bootstrapped T$_o$ estimates among walleye (*Sander vitreus*) populations spanning a large (ΔADD$_5$=1280, *n*=25) and a small (ΔADD$_5$=155, *n*=81) thermal range. Panel (a) shows the mean coefficient of variation of observed walleye growth rates at each T$_o$ over a small (-,•) and large (--,◆) thermal range. Panel (b) shows the distribution of T$_o$ values given a small (dark grey) and large (light grey) thermal range.

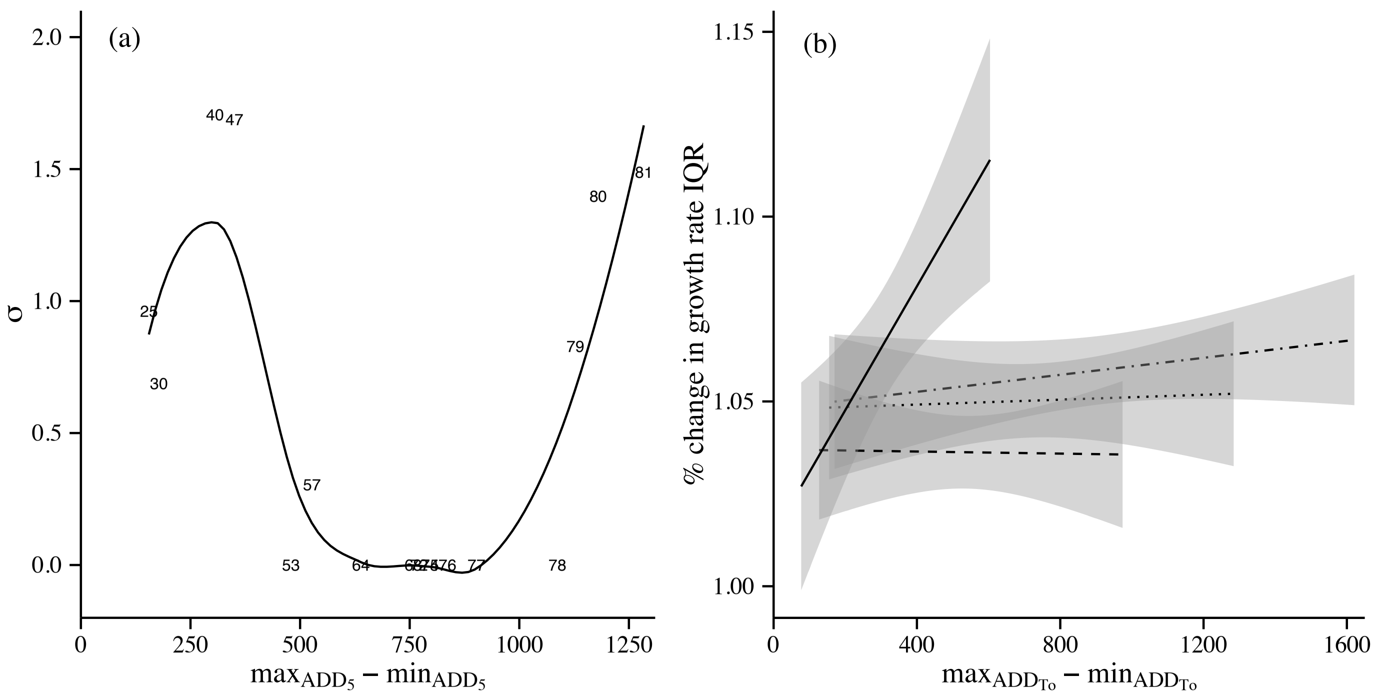

Figure 3.6 T_o estimation and apparent growth rates as a function of thermal difference among walleye populations in Minnesota and Ontario. Panel (a) shows how the standard deviation (σ) of 1000 bootstrapped T_o estimates change with thermal difference among populations. Relationship depicted using LOESS smoother ($\alpha = 0.7$) Point values indicate the number of populations within a thermal group. Panel (b) shows how the growth rate interquartile range (IQR) changes with thermal difference among populations when using T_o values of 0 (•-•), 5 (•••), 10 (--) and 15ºC (-). Shaded areas are 95% confidence intervals.

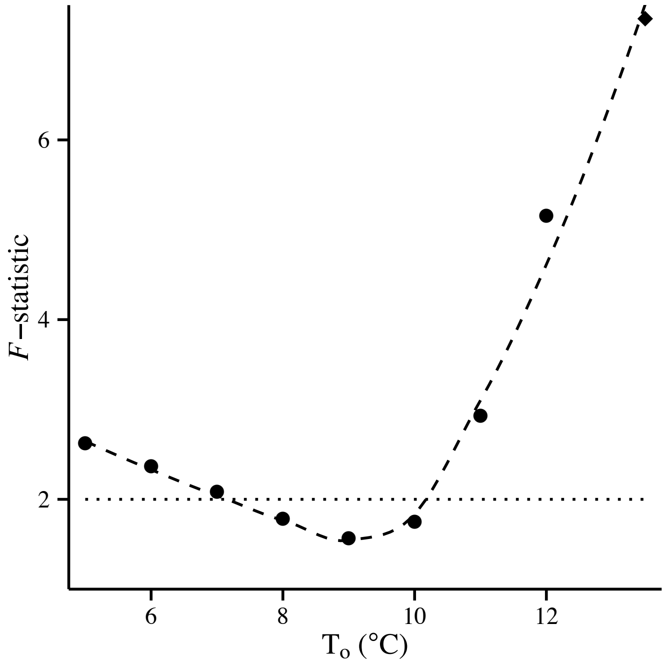

Figure 3.7 The effect of T_o on significance (Chow Test) when comparing growth model coefficient estimates of yellow perch in northern Alberta, Canada, (3 populations) to West Blue Lake in southern Manitoba, Canada. Fish and temperature data for West Blue Lake were obtained from Wong (1972) and data from Northern Alberta were digitized from Power and van den Heuval (1999). Missing temperature data from Sucker Lake were predicted using data from Kimowin Lake. The trend line (--) is via a LOESS smoother ($\alpha = 0.85$) and the horizontal line indicates the significance threshold (•••). This re-analysis of Power and van den Heuvel (1999) shows that a significant difference in growth is detected at $T_o > 10$°C and < 8°C and these differences are more likely detected at high T_o. The original T_o used in Power and van den Heuvel (1999) was 13.5ºC (◆).

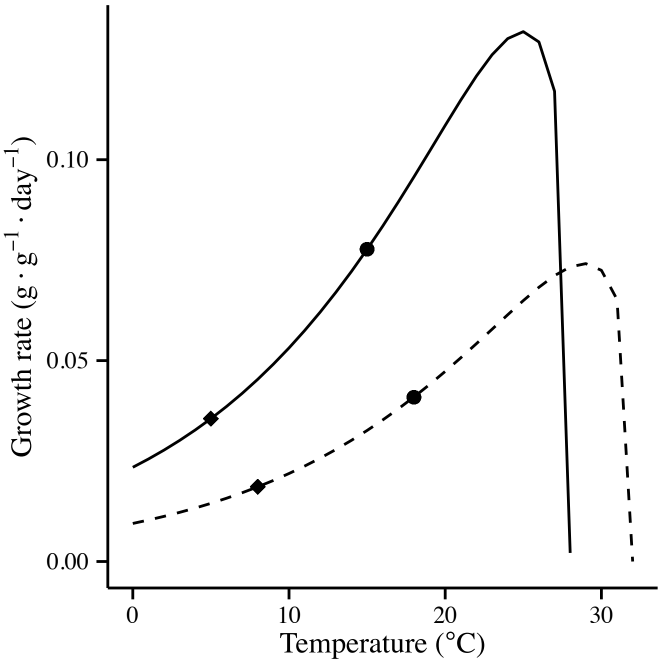

Figure 3.8 Application of the "10ºC rule" for estimating T_o (Charnov and Gillooly 2003) to growth rates of juvenile walleye (-) and yellow perch (--) as predicted by the Wisconsin Bioenergetics model (Hanson et al. 1997). Dots are mean development temperatures (15 and 18ºC for walleye and yellow perch, respectively) and diamonds are estimated T_o values (5 and 8ºC, respectively).

Chapter 4

General discussion and future directions

Degree-days (DD_{To}; ^{o}C·days) quantify the thermal experience of an organism and can be used to accurately and precisely describe growth and development in ectotherms. Understanding the underlying mathematical and statistical properties of degree-days is paramount in appropriately using this metric to further elucidate biological processes such as fish growth. Accounting for these underlying properties allows for the discernment of results that reveal biological phenomena from those that are simply mathematical or statistical artifacts.

Research in the fields of agronomy and entomology has identified and accounted for some of the mathematical properties of degree-days. For instance, the 'historical' method for calculating a single degree-day (i.e., $DD = \left[\frac{T_{Max}+T_{Min}}{2}\right] - T_o$) assumes the shape of a 24 hour temperature curve to be approximated by a rectangle and that an annual temperature curve is the aggregate of these rectangular degree-days (Legg 1998a); however, both daily and annual degree-days are better approximated by a sine curve (Arnold 1959). That said, using a sine curve to approximate a temperature curve can introduce a bias that varies geographically (Pruess 1983) due to extremes in humidity, temperature and variability in season length (Allen 1976). Although corrections for this bias have since been developed (e.g., Allen 1976), the relationship between degree-days and the fundamental mathematical underpinnings of the temperature curve (i.e., sine curve) itself has received limited attention.

Degree-day calculations incorporate a lower temperature threshold (T_o) because ectotherm growth is negligible at low temperatures. These values are likely species-specific and may even be population-specific in cases where local adaptation has occurred. Research in entomology and agronomy has developed procedures for estimating lower temperature thresholds (e.g., Arnold 1959, Thomson and Moncrieff

1982, Lysyk 1989 and Legg 1998a) but T_o estimates for species and populations among and within methods remain somewhat variable. For instance, Yang et al. (1995) noted that Arnold (1959) reported a T_o of 6ºC for corn in 1954 and a T_o of 4.3ºC in 1955. Reported T_o are also quite variable in fish science; however, unlike entomology, T_o values are typically unjustified or loosely defined as the lower temperature limit of some physiological or abiotic process (e.g., Hamel et al. 1997, Venturelli et al. 2010).

To date, very little has been done to quantitatively define threshold temperatures in fish science, nor have studies been conducted to understand the effect of a given T_o on our ability to accurately describe growth. The objective of this study was to determine the effect of T_o on our ability to use degree-days to account for growth within and among populations. In this study, I used hypothetical and empirical temperature and fish data to show that, although degree-days from different T_o values account for variation in immature growth within a population nearly equally well, accurate T_o identification becomes important when comparing growth among populations that are distributed across a wide thermal range. These results stem from the underlying mathematical and statistical properties of degree-days. Specifically, interaction between T_o and the sine curve.

In Chapter 2 I used hypothetical and empirical data to explore the importance of T_o when describing growth within a population. I first demonstrated that degree-days at different T_o values are highly correlated when T_o values are low, but become increasingly dissimilar as T_o nears the maximum annual temperature. I then gathered length-at-age data for eight species, collected by the natural resource agencies of Ontario and Minnesota, and demonstrated that this correlative property of degree-days at low T_o is why degree-days at low T_o are all able to account for much of the variation in immature growth within a single population. Simply, because degree-days are very similar among low T_o, they account for growth almost equally well. However, at high T_o, degree-days become increasingly dissimilar and their ability to account for growth declines similarly. Importantly, I demonstrated that this correlative property is directly a result of the shape of the temperature curve (which is essentially a sine curve), and is why effective T_o

values have little to do with growth limitations at temperatures approaching 0ºC.

In Chapter 3 I demonstrated that, although T_o matters little when accounting for growth within a single population, T_o becomes increasingly important when comparing growth among populations that have very different temperature curves. Initially, I demonstrated the affect of T_o on apparent growth by building model populations that experienced similar temperature dependent growth but had very different thermal experiences. By then corroborating the results of these simulations with empirical analyses using immature walleye (*Sander vitreus*) length-at-age data spread throughout Minnesota and Ontario, I was able to show that i) growth rates become increasingly biased as our chosen T_o becomes increasingly dissimilar from the 'true' value and ii) this bias increases with increasing thermal differences among comparative populations. This affect of T_o on growth rates is a direct result of the proportional inequalities that exist among populations with disparate temperature curves. These results have significant implications for studies comparing growth over large spatial scales because an inappropriate T_o value can lead to artificial apparent differences among populations over a latitudinal gradient (i.e., the appearance of counter-gradient growth).

Although this study has clarified some of the mathematical constraints of the degree-day, more research will be required in order to maximize its utility in fish science. Initially, further work is needed to determine how degree-days derived from air and water temperatures are correlated and how this relationship changes with T_o and latitude. As latitude increases, the relationship between air- and water-derived degree-days may become non-linear. This could result in an artificial latitudinal affect on apparent growth that is similar to using an inappropriate T_o. Similarly, although immature fish growth and degree-days are linearly related when viewed on an annual time-step, it is unclear if this remains true when incorporating mid-season growth data. Fish growth is well understood to be linear over a midrange of temperatures, but it becomes non-linear at the extremes (e.g., Edsall 1993). Because of these non-linear regions, it is unclear whether growth continues to aggregate in a linear manner with degree-days over the entire course of a season. Lower and upper temperature thresholds may be required to ensure a linear model that is not confounded by the curtailing of growth at the thermal limits of a species.

Additional effort is also needed to further standardize degree-days in fish science. Although this study takes the first steps by advising the use of standard T_o values (i.e., 0, 5, 10, and 15ºC), standard methods for identifying T_o should also be developed. Method standards should include statistical power requirements (e.g., size of *n* and extent of thermal range) for estimating T_o at various developmental stages. Furthermore, standardized methods should take into account and validate the findings of prior research conducted in terrestrial systems. For instance, Legg (1998b) showed that the least variability method for lower threshold estimates is biased towards low T_o. An example of a least variability method is the iterative search for the T_o that minimized the coefficient of variation in growth rates among waterbodies (Chapter 3) and r^2 method (Chapter 2). Findings such as these should be validated in aquatic systems. Moreover, although this study offers a method for converting degree-days among T_o (Chapter 2), these equations are unable to convert among all T_o and are limited by thermal range. Given that temperature curves are well approximated by a sine curve (Arnold 1959), it should be possible to use a sine curve to convert over a wider latitudinal gradient. This would facilitate standardization and thus future comparative studies.

Apart from the mathematical, statistical and methodological research that is required, we also need to better understand the relationships between the degree-day approach and the biological systems that it measures. For instance, understanding how well air temperature accounts for growth in cold-water species may reveal the significance of direct (i.e., metabolism) and indirect (i.e., primary production) affects of temperature on growth. Furthermore, very little is known about species-specific T_o values in aquatic systems. This includes determining whether general species characteristics, such as thermal preference (Hokanson 1977, Magnuson et al. 1979), can be used to group species by standardized T_o values, and if the "10ºC rule" (Charnov and Gillooly 2003) provides a reasonable estimate of T_o. Similarly, it is unclear if T_o changes with developmental stage within a species. Charnov and Gillooly (2003) suggest that because T_o falls 10ºC below the mean developmental temperature, theoretically the values are stage dependent. Yet it is unclear how variable these values are and whether a standard T_o would be equally informative.

By understanding the specificity and implication of T_o, it becomes possible to quantify the number of degree-days to different developmental stages, allowing for interesting conspecific and heterospecific comparisons of growth and development over spatial and temporal scales. For instance Neuheimer and Grønkjær (2012) determined that the number of degree-days to maturation has declined in North Atlantic cod (*Gadus morhua*) over the past three decades. Using degree-days to account for annual temperature variability, the study concluded that the decline in age at maturation was due to intense fishing pressure, and is an example of fisheries-induced evolution. Pursuing studies such as these would greatly enhance growth models and our understanding of climate on fish biology.

Given that this study focused on temperate climates and freshwater habitats, it is unclear how transferable my findings are to arctic, tropical or marine systems. In environments that are thermally stable and uniform (e.g., tropical), calendar time and degree-days tend to explain growth and development approximately equally well (Neuheimer and Taggart 2007). This equality arises because in thermally stable and uniform environment, temperature variability is low such that degree-days aggregate parallel to calendar time. Similarly, as the thermal environment over a species range becomes increasingly uniform (i.e., tropics and arctic), the affect of T_o on growth rates among populations is likely to become unobservable and T_o identification less important., as differences in apparent growth rates brought about by T_o are a result of differences in the temperature profiles among populations. Species distributed longitudinally are likely to see greater thermal uniformity than those distributed latitudinally. Unlike freshwater fish, which are confined to discrete inland waterbodies, marine populations are able to behaviorally thermo-regulate over great distances. Determining how similar the thermal experiences of marine populations are will determine the importance of such factors as T_o when comparing growth. This issue is even more complicated for anadromous species, which may experience extreme thermal differences during some life stages but not others.

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